

African tree species, *P. obliquum* is variable in leaf-shape (leaflets in this case) and some of this variation is correlated with geography.

Geographical variation is illustrated in fig. 2, which shows that there is a fairly well-defined pattern, in that the range of variation encountered in area 1 lies entirely outside that shown in areas 5 and 6. Populations in areas 2-4, however, which occupy an intermediate geographical position, provide connecting links. If these intermediates did not exist a taxonomist might be inclined to establish a northern and a southern subspecies or even two full species. But the overall pattern, in my opinion, is too diffuse to warrant the formal recognition of more than one taxon.

II. DISTRIBUTION AND ECOLOGY OF *PTAEROXYLON OBLIQUUM*

The overall distribution of *Ptaeroxylon obliquum* is large, extending from the East Usambara Mts. in the north to the Sundays River valley and the Bavianskloofberge in the south, and from near the Atlantic coast in the west to the coastal plain of Zululand in the east. It is however absent from most of this huge area because of two wide intervals in its distribution, namely the Barotseland-Kalahari interval in the interior of southern Africa and the Malawi interval in the central part of the upland and montane ridge which runs in an irregular fashion almost the whole length of Africa in the east. Because of these intervals, *P. obliquum* is confined to three relatively small areas of very different size (Fig. 2 and Appendix 1).

P. obliquum occurs in five of the regional phytochoria of the "Vegetation map of Africa" (WHITE, 1983a) but is only widespread and abundant in one, the Tongaland-Pondoland regional mosaic. Further information is given in Appendix 2 and is briefly summarized below.

Zambeian regional centre of endemism (II).

Apparently absent from typical Zambeian vegetation and only known from a few localities at the western and southern extremities of the region in W. Angola, SW Zimbabwe, E. Botswana and N. Transvaal. Mainly in rocky places. In semi-evergreen bushland and thicket, sometimes with emergent trees up to 20 m tall.

The Somalia-Masai regional centre of endemism (IV).

Only known from the West Usambara Mts. in Tanzania where it occurs as a rare member of 9-15 m tall semi-evergreen scrub-forest dominated by species of *Commiphora* and candelabra Euphorbias in the ecotone between typical Afromontane and typical Somalia-Masai vegetation.

The Afromontane archipelago-like regional centre of endemism (VIII).

North of the Limpopo only known from relatively dry *Juniperus procera* forest in the West Usambara Mts., Tanzania. In South Africa it is widespread in montane forest on the seaward slopes of the Drakenberg and further south in the Amatola Mountains and other ranges. It is more characteristic of the drier forests and the drier habitats within the wetter forests, but it can occur in the canopy of forest 30 m or more tall where the rainfall is up to 1875 mm *per annum*.

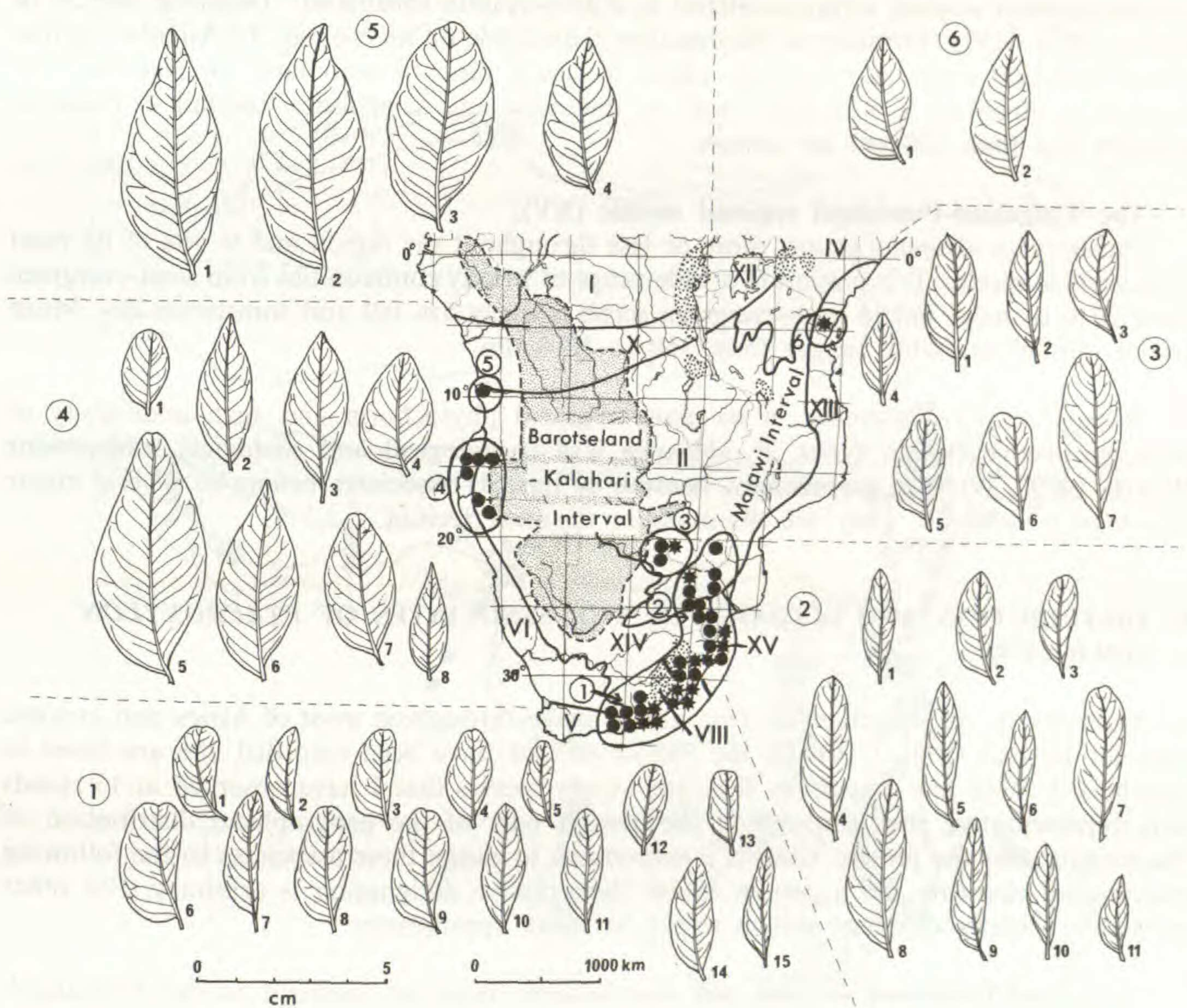


Fig. 2. — *Ptaeroxylon obliquum* : Pictorialized distribution map showing : variation in leaflet shape, the distribution of Kalahari Sand (stippled), the Barotseland-Kalahari and Malawi intervals, and the regional phytochoria of WHITE (1983a; for their names see legend of fig. 1). One symbol is shown for each degree square within which *Ptaeroxylon* is known to occur; circles represent herbarium specimens whereas stars indicate degree squares in which the author has studied its ecology. The leaflets were drawn from the following specimens : 1.1. Dyer 2024, 1.2. Acocks 9693, 1.3. Story 2786, 1.4. Paterson 2217, 1.5. Sim 2175, 1.6. Sim 3856, 1.7. Ecklon & Zeyher s.n., 1.8. Britten 2072, 1.9. Long 706, 1.10. Forest Department 5533, 1.11. Cruden 79, 1.12. Dyer 658, 1.13. Sim 1441, 1.14. Forest Department 5454, 1.15. Galpin 8097, 2.1. Repton 700, 2.2. Barbosa 721, 2.3. Gomes e Sousa 3974, 2.4. Pentz 219, 2.5. O.S.V. 118, 2.6. Hornby 2816, 2.7. Bayer 8438, 2.8. Van der Schijff 511, 2.9. Ward 2931, 2.10. Gomes e Sousa 3693, 2.11. Pole Evans s.n., 3.1. Armitage 186, 3.2. Pole Evans 3237, 3.3. Savory 501, 3.4. Steedman 162, 3.5. Sim 19224, 3.6. Orpen 6/50, 3.7. Pole Evans 3264, 4.1. Santos & Henriques 400, 4.2. Andrade 60, 4.3. Santos & Henriques 420, 4.4. Torre 8838, 4.5. Teixeira & Santos 3864, 4.6. Teixeira 490, 4.7. Santos & Henriques 420, 4.8. Welwitsch 1694, 5.1. Gossweiler 9185, 5.2. Cameira 72, 5.3. Pereira 297, 5.4. Welwitsch 1693, 6.1. & 2. Ross 593.

The Kalahari-Highveld regional transition zone (XIV).

Only recorded from the north-western extremity where it occurs in the "Transition from *Colophospermum mopane* scrub-woodland to Karoo-Namib shrubland" (mapping unit 36 of WHITE, 1983a : 191). Virtually no information is available on its ecology. In Angola it grows among subdesert rocks and in rocky places in sparse mopane woodland. In Namibia it is found as a shrub up to 4m high, both on limestone and sandstone. Rainfall in places is probably less than 250 mm *per annum*.

The Tongaland-Pondoland regional mosaic (XV).

Ptaeroxylon obliquum occurs more or less throughout the region and is one of its most characteristic species. It is present in a wide range of woody communities from semi-evergreen forest 20 m or more tall to semi-evergreen scrub scarcely 5 m tall and sometimes less. Mean annual rainfall probably ranges from 350 to 1300 mm.

Because of its occurrence in so many regional phytochoria and such a diversity of physiognomic vegetation types, *P. obliquum* is a chorological and ecological transgressor (WHITE, 1979 : 39). Not surprisingly, because of this, its associates belong to several major chorological elements. They are discussed in the next section.

III. DISTRIBUTION AND ECOLOGY OF THE ASSOCIATES OF *PTAEROXYLON OBLIQUUM*

Collectively, the associates of *Ptaeroxylon* range throughout most of Africa and in some cases far beyond (Figs. 1-19). Of the 500 or so that have been recorded 206 are listed in Appendix 2. With few exceptions they are woody species that I have observed at 15 stands from representative sites throughout the greater part of the geographical distribution of *Ptaeroxylon*. For the present study it is convenient to assign these associates to the following chorological elements. To a certain extent their precise designation is arbitrary. For other analyses a slightly different system might be more appropriate.

Tongaland-Pondoland endemic and near-endemic taxa are confined to the Tongaland-Pondoland regional mosaic (WHITE, 1983a : 197), or extend only a relatively short distance into adjacent regions. They include *Buxus macowanii*, *Dahlgrenodendron* (monotypic, *D. natalense*), *Diospyros dichrophylla*, *D. inhacaensis*, *D. scabrida*, *D. villosa*, *Dombeya cymosa*, *Encephalartos altensteinii*, *Harpephyllum caffrum*, *Hippobromus pauciflorus*, *Protorhus longifolia*, *Stangeria* (monotypic, *S. paradoxa*), *Strelitzia nicolai*, *Umtiza* (monotypic, *U. listerana*, Fig. 4), and *Turraea obtusifolia* (Fig. 4).

Afromontane and sub-Afromontane endemic and near-endemic taxa. Afromontane taxa are limited to the archipelago-like Afromontane Region (WHITE, 1983a : 161); there are few species in this category. The majority of Afromontane species are near-endemics in that they are also represented elsewhere by small distant satellite populations or by local marginal intrusions into the adjacent phytochoria but the overwhelming majority of their individuals occur in Afromontane communities. Sub-Afromontane endemic and near-endemic taxa are

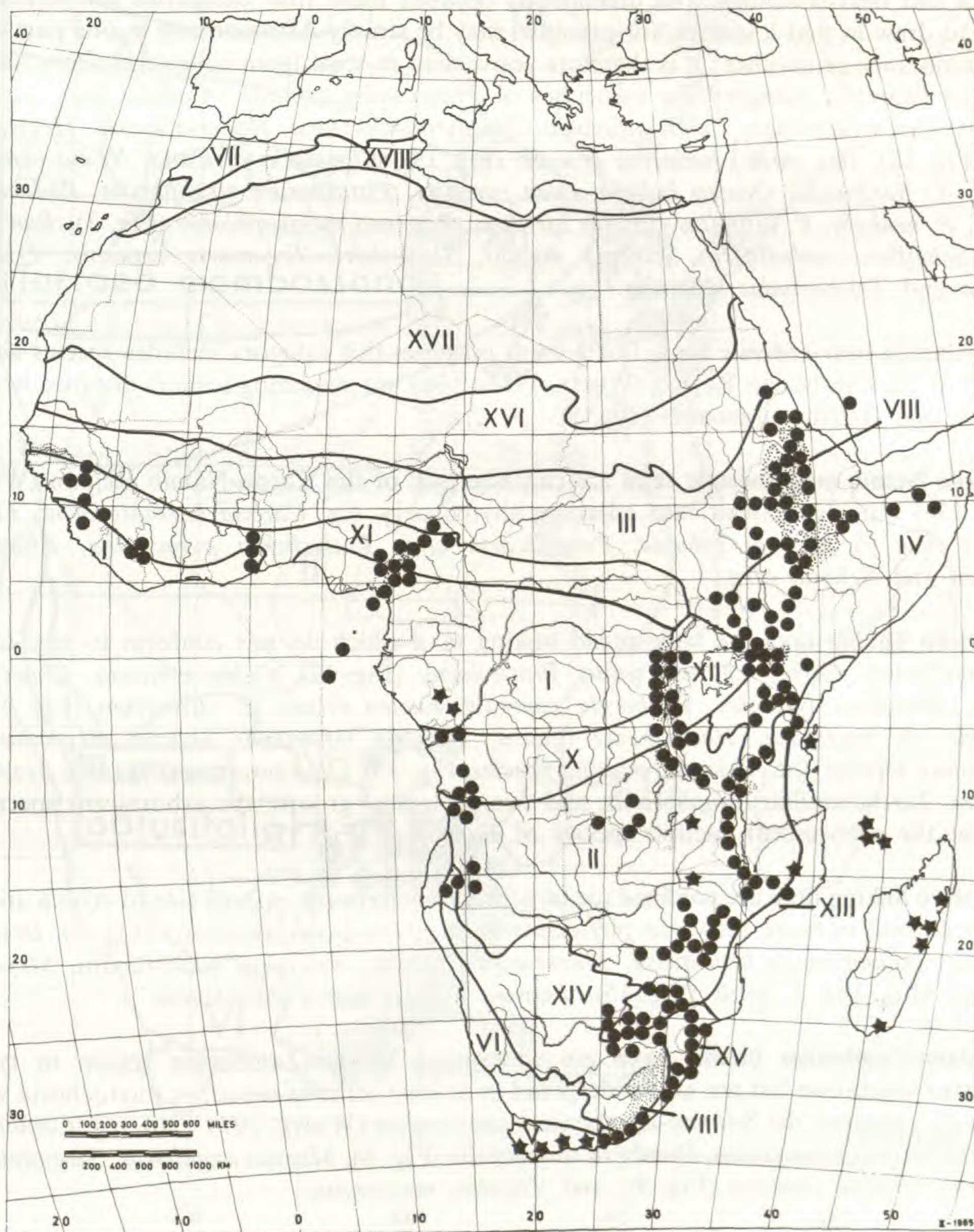


Fig. 3. — Combined geographical distributions of *Nuxia congesta* (circles, after LEEUWENBERG, 1975, simplified) and *Rapanea melanophloeos* showing only those localities outside the range of *Nuxia* (stars, after WHITE, 1984). Collectively these two species occur more or less throughout the Afrotropical Region, therefore except for a few distant satellite populations all Afrotropical tree species are confined to their collective area.

associated with montane vegetation but occur overall at lower altitudes than Afromontane endemics and near-endemics. The distinctions between these four categories are sometimes difficult to draw in that a species, for example, may be strictly Afromontane in one part of its sub-Afromontane in another; it is therefore convenient to treat them collectively here. In this range and collective category the associates of *Ptaeroxylon* include: *Calodendrum capense*, *Chrysophyllum viridifolium*, *Curtisia faginea*, *Diospyros whyteana*, *Halleria lucida*, *Heywoodia lucens* (Fig. 18), *Ilex mitis*, *Juniperus procera* (Fig. 19), *Kiggelaria africana*, *Nuxia congesta* (Fig. 3), *N. floribunda*, *Ocotea bullata*, *Olea capensis*, *Pittosporum viridiflorum*, *Podocarpus falcatus*, *P. henkelii*, *P. latifolius*, *Prunus africana*, *Rapanea melanophloeos* (Fig. 3), *Rawsonia lucida*, *Schefflera umbellifera*, *Scolopia mundii*, *S. zeyheri*, *Tecomaria capensis*, *Trichilia dregeana* and *Trichocladus ellipticus*.

Zambezian near-endemic taxa. For present purposes this category includes species almost confined to the Zambezian Region (WHITE, 1983a : 86) but extending a short distance beyond its limits, e.g. *Afzelia quanzensis* (Fig. 5).

Karoo-Namib near-endemic taxa are characteristic of the Karoo-Namib Region (WHITE, 1983a : 136) but also extend into adjacent phytochoria, e.g. *Carissa haematocarpa*, *Euclea undulata* (Fig. 6), *Grewia robusta*, *Portulacaria afra*, *Putterlickia pyracantha*, *Rhigozum obovatum* and *Schotia afra*.

African linking taxa are widespread linking taxa which do not conform to any of the categories listed above, e.g. the genus *Brachylaena* (Fig. 12), *Celtis africana*, *Chaetacme aristata*, *Diospyros lycioides*, *Ekebergia capensis*, *Euclea crispa*, *E. divinorum* (Fig. 6), *E. natalensis*, *E. racemosa*, *Heteropyxis* (genus, Fig. 16), *Maytenus undata*, *Myrothamnus flabellifolius*, *Obetia* (the African mainland species, Fig. 13), *Olea europaea* (Fig. 11), *Syzygium cordatum*, *Tarchonanthus camphoratus*, and two ecological groups, the arborescent species of *Aloe* and the arborescent cactoid species of *Euphorbia* (Fig. 17).

Eastern linking taxa are confined (or largely confined) to the eastern side of Africa and are well represented in more than one phytochorion, e.g. *Diospyros natalensis* (Fig. 7), *Drypetes natalensis*, *Inhambanella henriquesii*, *Macaranga capensis*, *Newtonia hildebrandtii*, *Strychnos henningsii* (Fig. 14), *S. mitis* (Fig. 15), *Turraea fischeri* and *T. floribunda*.

Sudano-Zambezian linking taxa are widespread in the Zambezian region in typical Zambezian vegetation but are also widespread in at least some of the other phytochoria which collectively comprise the Sudano-Zambezian super-region (WHITE, 1979 : 20), e.g. *Combretum molle*, *Dalbergia melanoxylon*, *Dombeya rotundifolia* (Fig. 8), *Maerua angolensis*, *Steganotaenia araliacea*, *Trichilia emetica* (Fig. 9), and *Ziziphus mucronata*.

Guineo-Congolian linking taxa are widespread in and characteristic of Guineo-Congolian vegetation (WHITE, 1983a : 71) but extend beyond the Guineo-Congolian transition zones into other phytochoria mainly in localized patches of relatively moist forest or in riparian forest, e.g. *Celtis gomphophylla*, *Croton sylvaticus*, *Morus mesozygia* (Fig. 10) and *Oncinotus tenuiloba*.

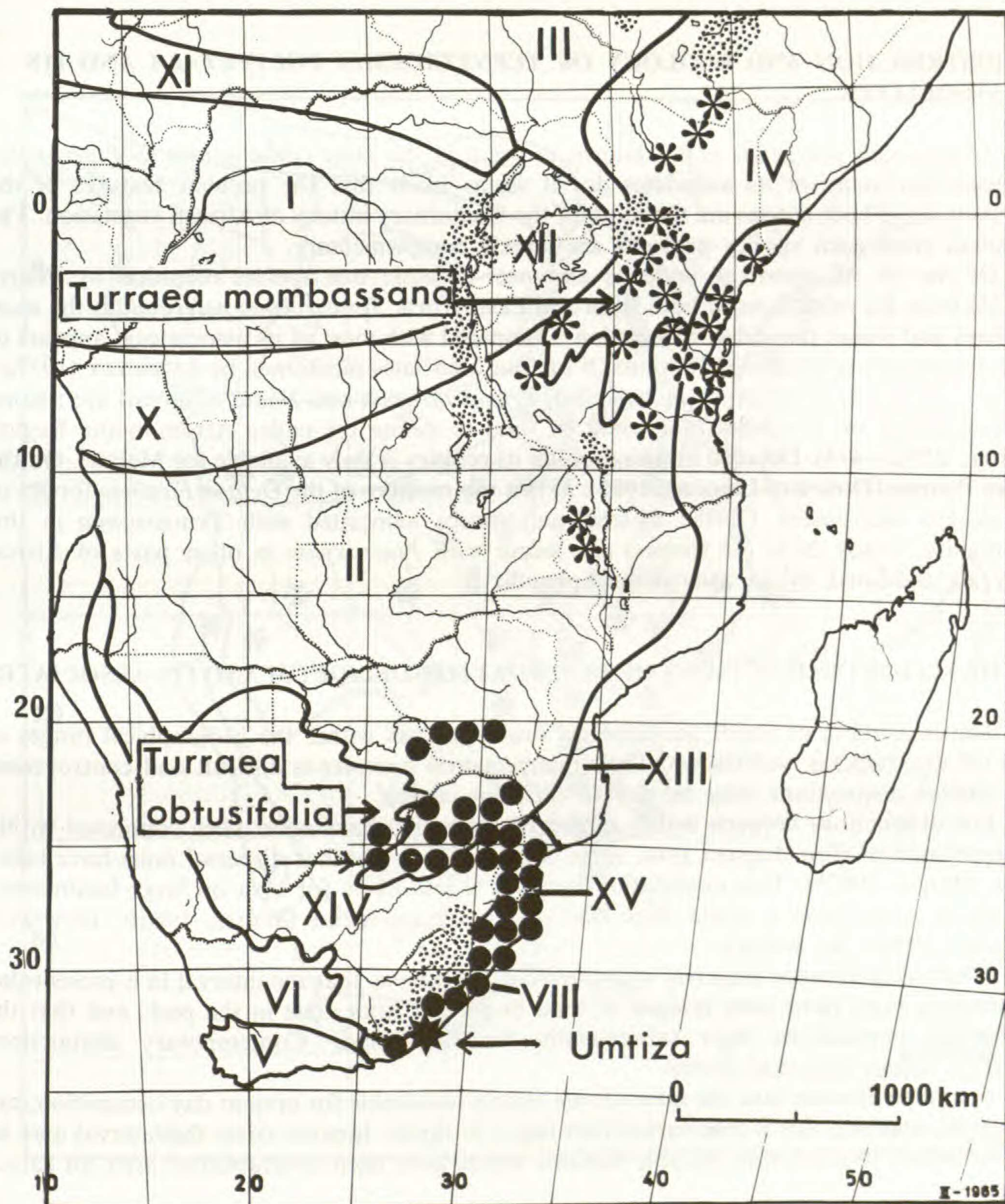


Fig. 4. — Distribution of : *Umtiza*, a monotypic (*U. listerana*) Tongaland-Pondoland endemic genus; *Turraea obtusifolia*, a Tongaland-Pondoland near-endemic species (WHITE, 1986 : fig. 3, updated); and its very closely related northern relative *T. mombassana*, an East African linking species (original). The distributions of nearly all Tongaland-Pondoland endemic and near-endemic species lie entirely within that of *T. obtusifolia*. — NOTE : the two subspecies of *T. mombassana* (STYLES & WHITE, 1989) are not shown separately.

IV. DISTRIBUTION AND ECOLOGY OF *TERNSTROEMIA POLYPETALA* AND ITS ASSOCIATES

Ternstroemia polypetala is not known to occur in the same communities as *Ptaeroxylon obliquum* but many of its associates do. It seems likely that the peculiar features of the distributions of both species are the result of the Quaternary history of African vegetation. The historical clues each species provides are largely complementary.

Of the 18 Afromontane endemic and near-endemic tree species recorded by WHITE (1983b) from the mountains of both West and East Africa, *Ternstroemia polypetala* is the most localized and shows the widest disjunction. Compared with most of its associates it appears to have a markedly relictual distribution. Of its four associates mentioned by LETOUZEY (1977a : 8), three (*Podocarpus latifolius (milanjianus)*, *Prunus africana* and *Nuxia congesta*) are among the assemblage of 12 species that could be used to define the entire Afromontane Region (WHITE, 1978a : 474). Detailed information on its ecology is only available for Malawi. On the Nyika Plateau (DOWSETT-LEMAIRE, 1985 : 351) it is a member of the *Ocotea-Ficalhoa* forests of the eastern escarpment. Of the 84 trees and shrubs associated with *Ternstroemia* in this community, nearly 20 % (16 species) also occur with *Ptaeroxylon* in other parts of Africa. They are indicated by an asterisk in Appendix 2.

V. THE MAJOR DISJUNCTIONS OF *PTAEROXYLON OBLIQUUM* AND ITS ASSOCIATES

The occurrence of major geographical discontinuities within the geographical ranges of taxa (of any rank) is well-known. Their interpretation however is difficult and controversial and similar disjunctions may be due to different causes.

For disjunctions between widely separated lands that have never been connected within the time span of their disjunct taxa, some degree of long-distance dispersal must have taken place (WHITE, 1983b). This explanation however is less likely for taxa on large landmasses, though in some cases it could have been an important factor (WHITE, 1983b; DOWSETT-LEMAIRE, 1988b, see below).

When long-distance dispersal is not involved, it follows that the interval in a present-day distribution must have been bridged at least in part at some time in the past, and that the connecting populations have subsequently become extinct. Contemporary disjunctions therefore reflect historical events.

For some disjunct taxa the intervals are clearly unsuitable for present day occupation, but the extent to which this is true varies from taxon to taxon. In some cases the interval may be due to failure to recolonize suitable habitats which have been re-established after an earlier extinction.

It is unlikely that there is a single simple historical explanation that can account for all disjunctions in the contemporary sub-Saharan African flora or even, in some cases like *Ptaeroxylon*, within a single species. The contemporary patterns are too complex for this but they are not chaotic and, despite the idiosyncracies of many taxa, some degree of underlying uniformity can be detected.

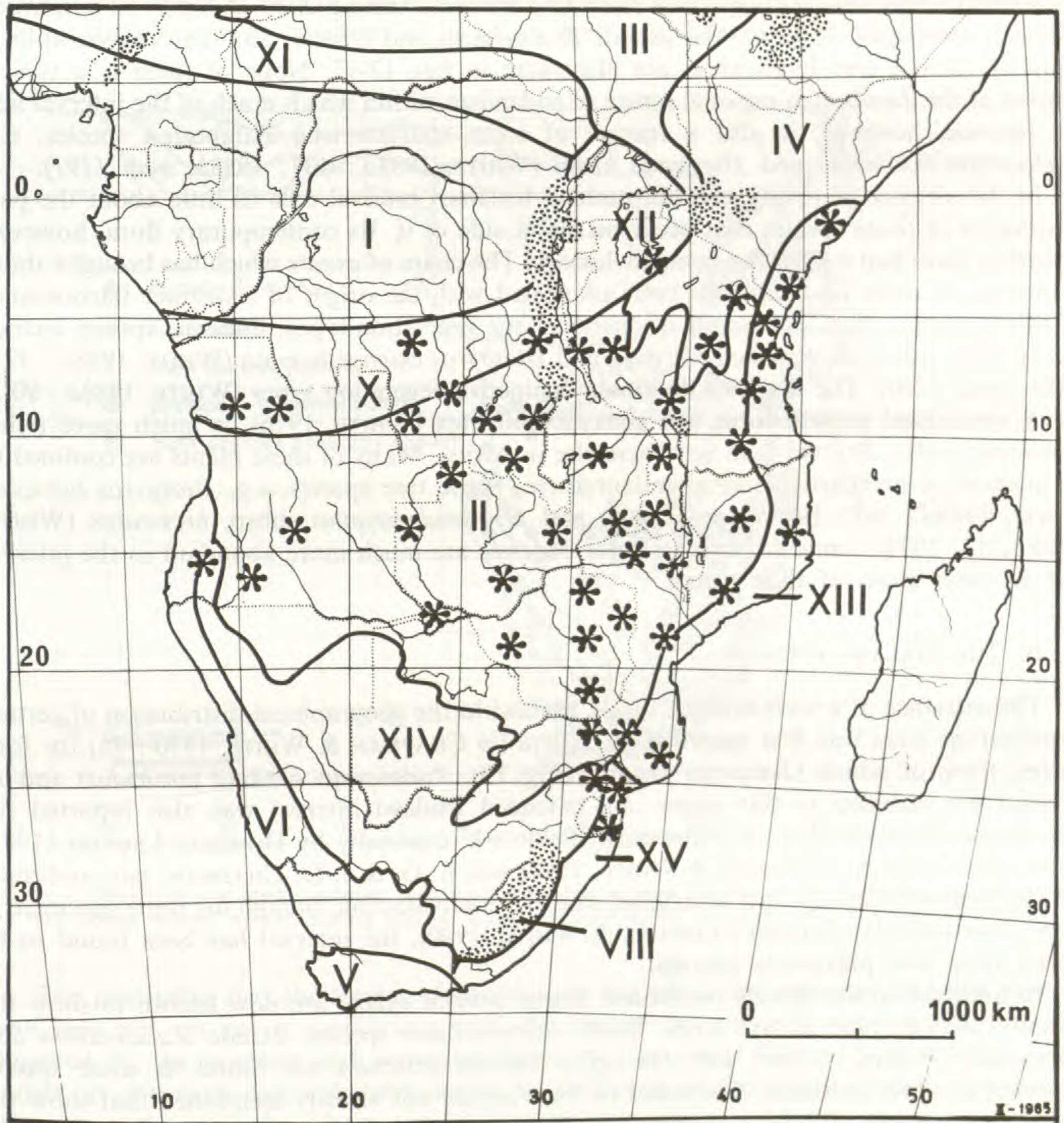


Fig. 5. — Generalized distribution of *Afzelia quanzensis*, a Zambezan near-endemic species which intrudes a short distance into the adjacent transition zones and mosaics (original).

A. THE BAROTSELAND-KALAHARI INTERVAL.

Several associates of *Ptaeroxylon* show this interval. Among them *Heteropyxis natalensis*, *Strychnos henningsii*, *S. mitis*, the genera *Brachylaena* and *Obetia*, and an ecogeographical group of cactoid tree Euphorbias are illustrated in figs. 12-17. None of them is a typical member of the Zambezian regional centre of endemism within which much of the interval lies. The interval, however, is also a feature of some characteristic Zambezian species, e.g. *Brachystegia floribunda* and *Diospyros kirkii* (WHITE, 1988a : 407; 1988b, map 1191).

In the absence of fossils, the Barotseland-Kalahari interval tells us little about the past distribution of those species that occur on either side of it. Its contemporary flora, however, appears to have had a long and complex history. The chain of events which has brought about an interval in some taxa has also been associated with the origin of a distinct Barotseland-Kalahari endemic flora and a suite of characteristic vegetation types. Endemic species include *Brachystegia bakerana*, *Baikiaea plurijuga* and *Diospyros chamaethamnus* (WHITE, 1988a : 391; 1988b : map 1210). The first two dominate distinctive vegetation types (WHITE, 1983a : 90 & 98). A specialized growth form, the geoxylic suffrutex (WHITE, 1976), is much more richly represented in the interval than anywhere else in Africa. Many of these plants are confined to the interval or are particularly abundant there. Some tree species, e.g. *Diospyros batocana* (WHITE, 1988a : 388; 1988b : map 1209) and *D. pseudomespilus* subsp. *brevicalyx* (WHITE, 1978b : 314; 1978c : map 481), though not endemic are much more abundant in the interval than in other parts of their range.

B. THE MALAWI INTERVAL.

The existence of a wide interval inside Malawi in the geographical distribution of certain Afromontane trees was first recorded by WHITE (in CHAPMAN & WHITE, 1970 : 76) for four species, three of which (*Juniperus procera* (Fig. 19), *Podocarpus henkelii* (*ensiculus*) and *P. falcatus*) are included in this paper. An extended Malawi interval was also reported for *Ptaeroxylon obliquum* (Fig. 2). Subsequent fieldwork, especially by DOWSETT-LEMAIRE (1985, 1988a, 1989; DOWSETT-LEMAIRE & WHITE, 1990) and E. G. & J. D. CHAPMAN, has confirmed that the Malawi interval is not an artefact due to undercollecting, though for some species, e.g. *Podocarpus henkelii* (DOWSETT-LEMAIRE & WHITE, 1990), the interval has been found to be shorter than was previously thought.

In addition to the species mentioned above, several others are now known to show the Malawi interval. Not all are trees. Small Afromontane species include *Zaluzianskia* and *Macowania* (WHITE, 1978a : 480, for refs.). Similar intervals are found in some species occurring at lower altitudes. Associates of *Ptaeroxylon* not already mentioned that show the Malawi interval are *Brachylaena* (Fig. 12), *Heywoodia lucens* (Fig. 18) and *Obetia* (Fig. 13). This interval is also reflected in the relative poverty in species of cactoid tree Euphorbias in Malawi and adjacent countries, and in their rarity there compared with their abundance and diversity further north and south (Fig. 17). Arborescent species of *Aloe* behave in a similar way.

The relative poverty of Malawi in floristic elements that are better developed further north and further south appears to be partly due to the present-day physical environment which does

not necessarily influence all species in the same way, and partly to historical causes. In general the mountains of Malawi are lower than many of those elsewhere on the eastern side of Africa or they are smaller, or (e.g. Mt. Mulanje) more isolated. The regional climate is also more seasonal with a single long dry season during which little or no rain falls and is only partly ameliorated by periodic invasions of moist air (*chiperoles*) from the Mozambique Channel.

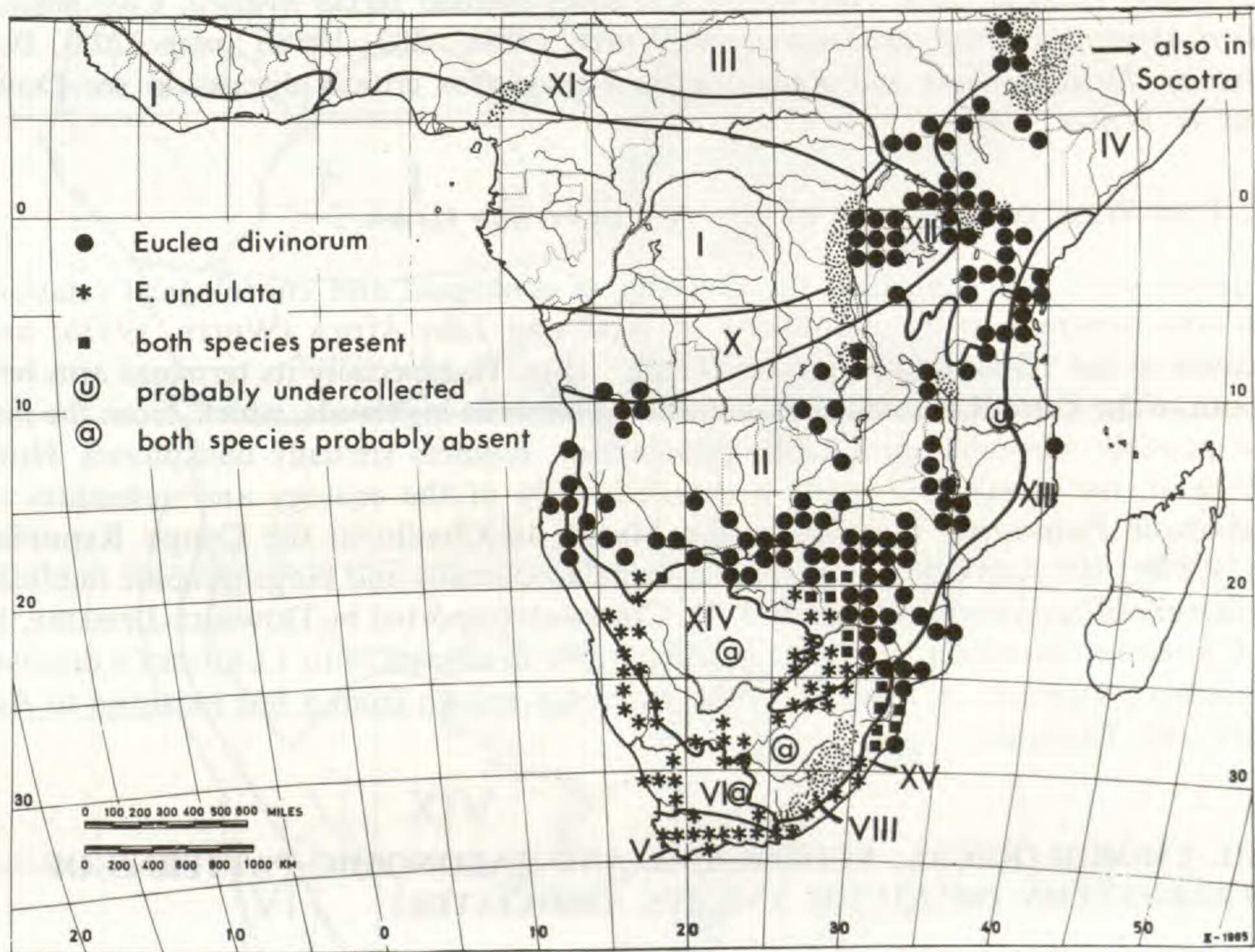


Fig. 6. — Distribution of *Euclea undulata*, a Karoo-Namib near-endemic species, and *E. divinorum*, a more northerly very closely related African linking species, which overlaps slightly in range with *E. undulata* (original).

The possibility that the forests of Malawi are not all of the same age and that some of them may not yet be in equilibrium with the present-day physical environment has been suggested by the botanist and zoologist DOWSETT-LEMAIRE (1989a : 127 & 1989b), whose studies are the most comprehensive yet to be published of their kind. In her own words : “Some hypotheses on the relative age of different forest areas in Malawi can be proposed by observing patterns of floristic diversity, physiognomy, and bird distribution... The most mature and species-rich communities are the Afromontane rain forests of the north, and some of the mid-altitude forests of the south, especially those of the southern slopes of Mt. Mulanje. These forests are situated on the more extensive or prominent mountain massifs, and have undoubtedly survived climatic vicissitudes better than elsewhere... By contrast, the... forests of the central highlands are in a state of incomplete regeneration from some past, probably not

too distant, destructive event. Recolonization of this area by forest birds from both north and south is in progress, but some obvious niches in the forests of Dedza and Chongoni are still not filled". Elsewhere (1988b : 273) she discusses the role of fruit consumers, especially birds (but also bats and monkeys) in the recolonization of upland areas by forest after the last interpluvial.

In common with the Barotseland-Kalahari interval, the Malawi interval has several (though fewer) endemic taxa. Noteworthy examples include *Buxus nyasica*, *Cola chlorantha*, *Diospyros abyssinica* subsp. *chapmaniorum* (WHITE, 1988a : 382; 1988b : map 1205), *Dovyalis spinosissima*, *Ficus modesta* and *Rawsonia burtt-davyi* (for critical discussion see DOWSETT-LEMAIRE & WHITE, 1990).

C. EAST-WEST DISJUNCTIONS IN THE AFROMONTANE FLORA.

Further work has confirmed the diversity of ecological and chorological relationships among taxa common to the mountains of West and East Africa (WHITE, 1983b) and the significance of the "Southern Migratory Track" (Fig. 1), especially its terminal arm between the mouth of the Zaire River and the Cameroun-Mambilla highlands, which, from the point of view of possible Afromontane satellite populations, remains virtually unexplored. However, MALEY et al. (in press) have made a detailed study of the ecology and associates of the population of *Podocarpus latifolius* in the Massif du Chaillu in the Congo Republic (see WHITE, 1983b : 105, and below) and discuss its palaeoclimatic and biogeographic implications. The discovery of *Anthonota noldeae* by J. D. CHAPMAN (reported by DOWSETT-LEMAIRE, 1989c) in the Cameroun-Mambilla highlands is comparable in interest with LETOUZEY's discovery of *Ternstroemia polypetala*. *A. noldeae* is otherwise only known from a few localities in Angola, E. Zaire and Tanzania.

VI. THE CHOROLOGICAL, ECOLOGICAL AND TAXONOMIC PATTERNS OF *PTAEROXYLON OBLIQUUM* AND ITS ASSOCIATES

Every plant species is unique in its distribution and ecology. This is true to a much greater extent than is realized by the authors of simple chorological and ecological classifications, or those who offer simple historical explanations of contemporary plant distributions. This is well illustrated by *Ptaeroxylon obliquum* and its associates, 206 woody species of which are referred to in the present paper. This figure represents fewer than half of those that have been recorded. The following account, however, is based on only 22 taxa (3 genera and 19 species), namely those whose distributions are shown in figs. 1-19. They are sufficient to illustrate my theme. What these species have in common is their association in at least some part of their geographical range with *Ptaeroxylon*. Collectively, in contrast to the restricted geographical area occupied by *Ptaeroxylon*, they occur throughout the greater part of Africa and sporadically far into Asia. A convincing historical explanation of this state of affairs is unlikely to be simple.

Figures 1-19 show that the 22 taxa collectively occur in all the regional phytochoria recognized by WHITE (1983a) for the African mainland, except for one, the Afroalpine, which ecologically is the most extreme and occupies the smallest area. Only the more striking

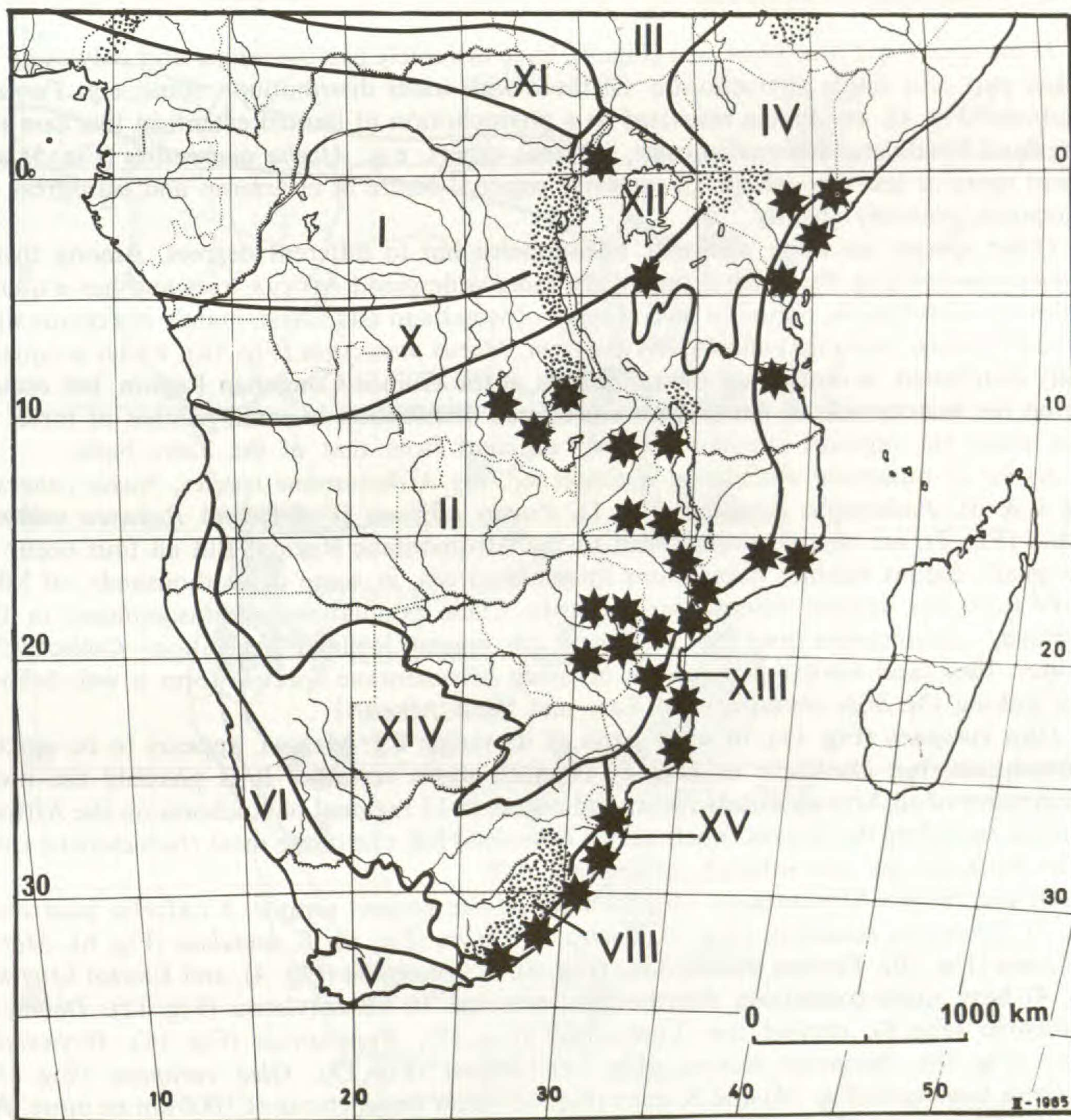


Fig. 7. — Distribution of *Diospyros natalensis*, an East African linking species (after WHITE, 1988b, map 1191, simplified).

patterns (and these are not mutually exclusive) are mentioned below. They can be matched in broad outline in many other taxa.

A. CHOROLOGICAL PATTERNS.

Some taxa, e.g. *Umtiza listerana* (Fig. 4), have extremely narrow ranges and only occur in a small part of a single phytochorion. Of those with wider distributions, some, e.g. *Turraea obtusifolia* (Fig. 4), are almost restricted to a phytochorion of limited extent, in this case the Tongaland-Pondoland regional mosaic, whereas others, e.g. *Afzelia quanzensis* (Fig. 5) are present more or less throughout an extensive regional centre of endemism and transgress its boundaries relatively slightly.

Other species are more markedly transgressive but to different degrees. Among them, *Trichilia emetica* (Fig. 9), which is one of the more widespread African trees and has a quasi-continuous distribution, occurs in several types of woodland and forest, mainly in regions with a broadly similar (savanna) climate. By contrast, *Morus mesozygia* (Fig. 10), which is equally widely distributed, is centred on the rainforests of the Guineo-Congolian Region, but occurs also on the eastern side of Africa with a scattered distribution in small patches of forest in areas where the regional climates are very different from that of the Zaire basin.

So far as numerical abundance is concerned, the Afromontane species, *Nuxia congesta* (Fig. 1 & 3), *Podocarpus latifolius* (Fig. 1), *Prunus africana* (Fig. 1) and *Rapanea melanophloeos* (Fig. 3), are overwhelmingly tied to the Afromontane Region. But all four occur in very small, distant satellite populations up to hundreds, in some cases thousands, of kilometres from the nearest Afromontane massifs. These populations are insignificant in the "lowland" phytochoria and do not occur in typical lowland vegetation. Collectively, however, they (and similar populations of other Afromontane species) form a well-defined track linking the high mountains of East and West Africa.

Olea europaea (Fig. 11), in some parts of its range, e.g. Malawi, appears to be strictly Afromontane, but elsewhere its ecology is much more versatile. It is possibly the most transgressive of all African woody plants and occurs in 13 regional phytochoria on the African mainland including the Sahara, where (as *O. laperrinei*) it is one of the most characteristic trees of the Saharan and sub-Saharan mountains.

Of the 18 non-Afromontane taxa included in the present sample, 8 (*Afzelia quanzensis* (Fig. 5), *Diospyros natalensis* (Fig. 7), *Euclea divinorum* (Fig. 6), *E. undulata* (Fig. 6), *Morus mesozygia* (Fig. 10), *Turraea mombassana* (Fig. 4), *T. obtusifolia* (Fig. 4), and *Umtiza listerana* (Fig. 4)) have quasi-continuous distributions, whereas 10 (*Brachylaena* (Fig. 12), *Dombeya rotundifolia* (Fig. 8), cactoid tree Euphorbias (Fig. 17), *Heteropyxis* (Fig. 16), *Heywoodia lucens* (Fig. 18), *Juniperus procera* (Fig. 19), *Obetia* (Fig. 13), *Olea europaea* (Fig. 11), *Strychnos henningsii* (Fig. 14) and *S. mitis* (Fig. 15)) show disjunctions of 1000 km or more. An extreme example is *Heywoodia* where the interval is 3000 km in length.

B. ECOLOGICAL PATTERNS.

Many of the widespread associates of *Ptaeroxylon*, like *Ptaeroxylon* itself, are versatile in their ecology regardless of whether their geographical range is "continuous" or disrupted. In different places they occur in communities which superficially appear to be very different. At

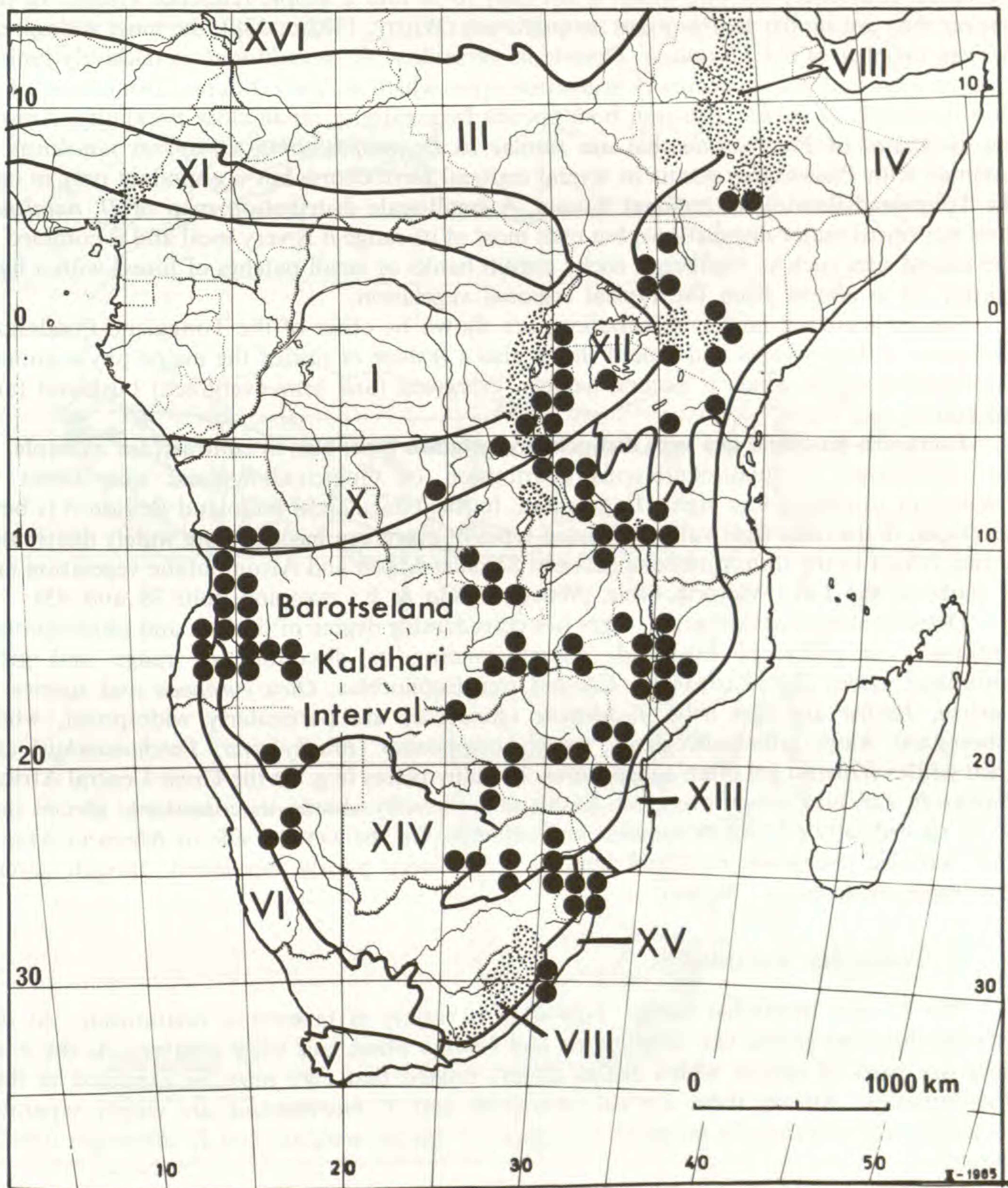


Fig. 8. — Distribution of *Dombeya rotundifolia*, a Zambezian linking species (after SEYANI, 1982).

first sight the situation looks chaotic but this is a false impression. There is an underlying ecological coherence, but one which is not easy to fit into a simple reference system. In this respect they are similar to *Diospyros mespiliformis* (WHITE, 1988a : 338), the most widespread African member of the *Ebenaceae*. Despite its versatility, *D. mespiliformis* is relatively limited in its ecology and always occurs in vegetation types which are very different from those of its closest relative, *D. kirkii*, although both species frequently occur in close proximity. Among the associates of *Ptaeroxylon* that are similar to *D. mespiliformis*, *Diospyros natalensis* in common with *Ptaeroxylon* occurs in several regional phytochoria but is abundant only in one, the Tongaland-Pondoland regional mosaic. A small-scale distribution map of *D. natalensis* does not reveal major disjunctions, but over most of its range it is very local and is confined to specialized sites such as inselbergs, rocky stream banks or small patches of forest with a light canopy. It is absent from the typical regional vegetation.

Similar scattered mosaic distributions are shown by other of the Tongaland-Pondoland associates of *Ptaeroxylon* and indeed this is also a feature of one of the major physiognomic vegetation types in which it occurs, namely, evergreen (and semi-evergreen) bushland (and thicket).

Evergreen bushland is a very distinctive vegetation type, but, in contrast, for example, to the continuous or quasi-continuous distribution of Guineo-Congoland rain forest or Zambezian woodland it is highly fragmented. In the Tongaland-Pondoland Region it is best-developed in the deep river valleys. Related types of evergreen bushland are widely distributed in east Africa in the transition zone between Somalia-Masai and Afromontane vegetation and in parts of the Lake Victoria basin (WHITE, 1983a & b : mapping units 38 and 45).

Despite much local variation, there is a considerable degree of floristic and physiognomic uniformity in evergreen bushland, notwithstanding its discontinuous range and great latitudinal extent (22° N to 34° S). Cactoid tree Euphorbias, *Olea europaea* and species of *Carissa*, *Euclea* and the tribe *Toddalieae* (*Rutaceae*) are particularly widespread, whilst arborescent Aloes, other succulents, woody composites (*Brachylaena*, *Tarchonanthus*) and giant nettles (*Obetia*) are often conspicuous. In many places (e.g. on the Great Central African Plateau in Zambia), where evergreen bushland is virtually absent, its constituent species may occur sporadically on termite mounds or inselbergs. On the western side of Africa in Angola and Namibia evergreen bushland appears to be very poorly developed, though several important elements are present.

C. TAXONOMIC PATTERNS.

The 22 taxa illustrated in figs. 1-19 show a variety of taxonomic relationship. At one extreme there are genera like *Heteropyxis* and *Umtiza* which lack close relatives. At the other there are pairs of species which are so closely related that care must be exercised in their discrimination. Among them *Turraea obtusifolia* and *T. mombassana* are widely separated geographically whereas the geographical ranges of *Euclea undulata* and *E. divinorum* overlap slightly.

Species also differ in their patterns of internal variability. Some, e.g. *Euclea divinorum*, are not very variable; some, e.g. *Turraea mombassana* show subspecific differentiation, whereas in others the variation pattern is so chaotic that a special category, the ochlopecies, is necessary to accommodate them, e.g. *Diospyros natalensis* (WHITE, 1962 : 79; 1988a : 343 & 432).

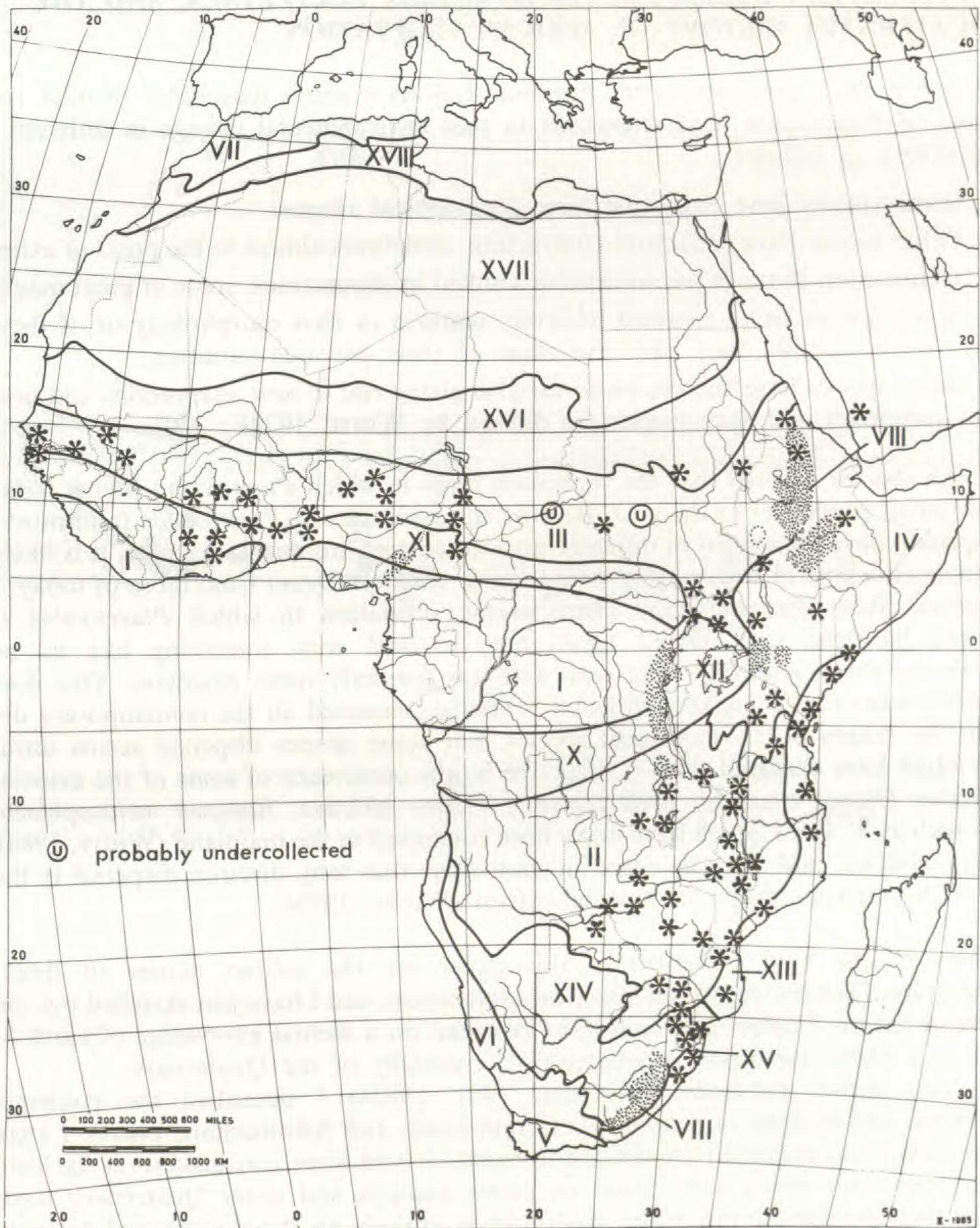


Fig. 9. — Distribution of *Trichilia emetica*, a Sudano-Zambezian linking species (after DE WILDE, 1968, map 4, simplified and updated).

VII. *PTAEROXYLON OBLIQUUM*, *TERNSTROEMIA POLYPETALA*, AND THE QUATERNARY HISTORY OF AFRICAN VEGETATION

From the facts presented in the previous sections it seems reasonable to infer that the associates of *Ptaeroxylon* have responded to past environmental change in different ways, among others, as follows :

1. Some species have expanded their geographical ranges.
2. Other species have undergone contraction, sometimes almost to the point of extinction.
3. Contraction of range has sometimes resulted in disjunctions, some of great magnitude.
4. Some species have remained relatively uniform in their morphology or, if they were formerly more variable, they have lost some of their previous variation.
5. Some species have become more variable giving rise to new adaptations and new taxa such as subspecies and semi-species (as defined by WHITE, 1978b : 250).

It can also be inferred that the vegetation types in which *Ptaeroxylon* occurs today had some different properties in the past. Because the associates of *Ptaeroxylon* (and most other plant species) have responded in different ways to past environmental change, it is likely that the former associates of *Ptaeroxylon* were to some extent different from those of today. But it also seems, likely that the most characteristic vegetation in which *Ptaeroxylon* occurs (evergreen bushland and related types) has persisted with something like its present physiognomy for a relatively long time and was formerly more extensive. This does not necessarily mean that evergreen bushland formerly connected all the contemporary disjunctions in the ranges of its constituent species. For some species dispersal across unsuitable terrain might have occurred. This is suggested by the occurrence of some of the associates of *Ptaeroxylon* (*Nuxia congesta*, *Olea capensis*, *Prunus africana*, *Rapanea melanophloeos*) on islands such as S. Tomé which have never been connected to the mainland (WHITE, 1984). It is unlikely, however, and in some cases inconceivable, that long distance dispersal is the sole cause of disjunctions within continental Africa (WHITE, 1983b).

Facts of the kind presented in this paper are the subject matter of descriptive biogeography. They cry out for an historical explanation, and I have just sketched out one of a very broad nature. Further precision must be based on a factual knowledge of earth history and of past biotas (historical biogeography), especially of the Quaternary.

In two earlier publications (WHITE, 1981, 1983b) I described the contemporary distributions and ecology of some lowland rain forest and Afromontane plants. I suggested that the facts I had presented are difficult to reconcile with some conclusions on the history of African vegetation which were based on pollen analysis and other Quaternary studies.

The facts included in this paper, based almost entirely on *Ptaeroxylon* and its associates, cover almost the whole of Africa and support the earlier conclusions which were based on a smaller area. Additional confirmation has come from further study of the Afromontane flora, especially *Podocarpus latifolius*, and from palaeopalynology. A more comprehensive review of the interdependence of descriptive and historical biogeography, in an African setting, might

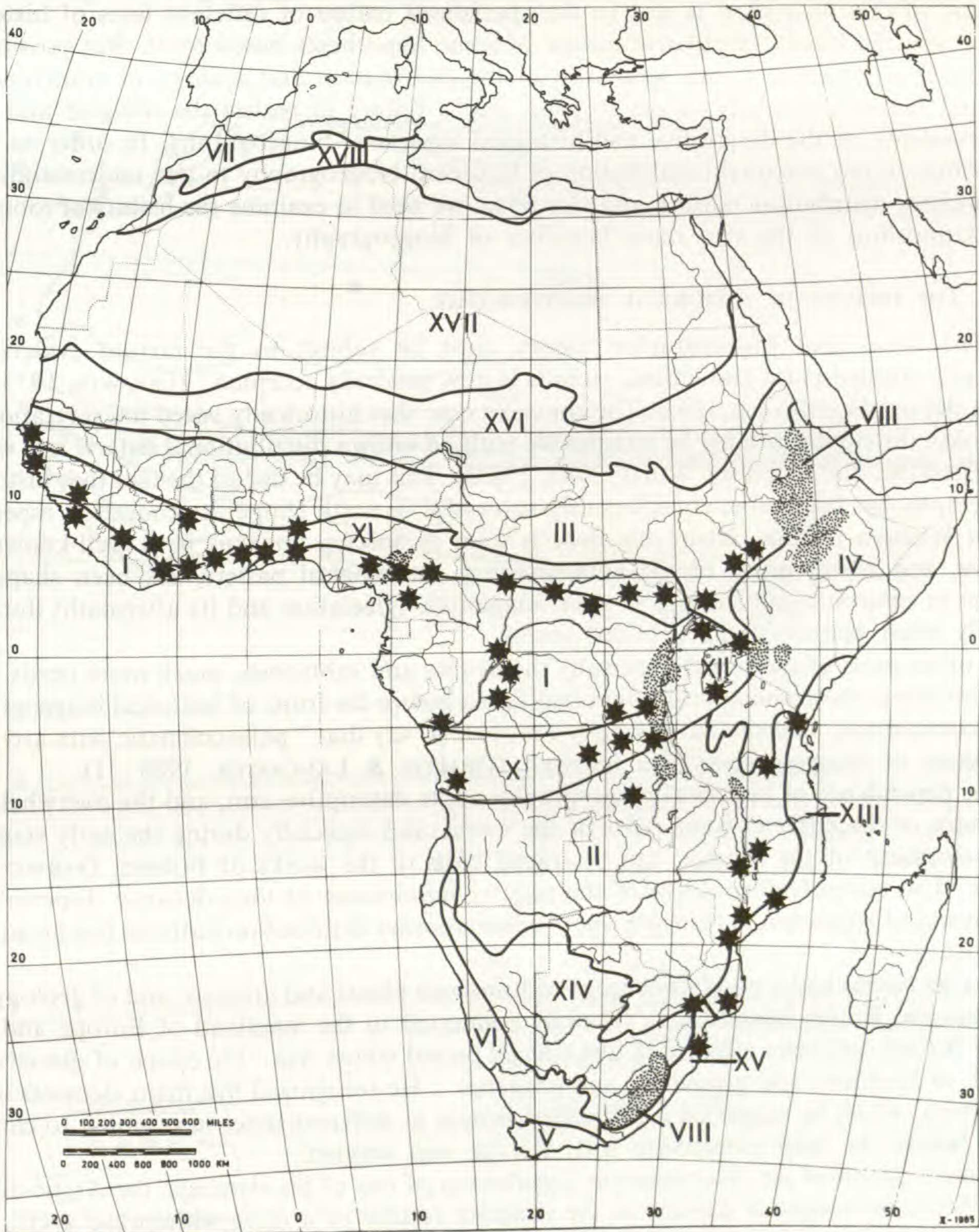


Fig. 10. — Distribution of *Morus mesozygia*, a Guineo-Congolian linking species (after BERG, 1977, fig. 14, simplified and updated).

now be appropriate. A lot has been discovered about the Quaternary in recent years but there is also much controversy, the roots of which are pre-Darwinian.

Some of this dissension is due to the specialized nature of different lines of historical evidence and the highly speculative nature of some hypotheses based on it. But possibly of even greater significance is our ignorance of the distribution and ecology of contemporary floras and faunas (especially in the tropics), and a failure to realize the obligate and total interdependence of the descriptive and historical aspects of biogeography. In order to get a clear picture of the potential contribution of historical biogeography to our understanding of contemporary distribution pattern and *vice versa*, we need to examine the historical roots and inter-relationships of the two main branches of biogeography.

A. THE HISTORY OF HISTORICAL BIOGEOGRAPHY.

“The thesis that biogeographic theory must be subject to the factual evidence of historically attested plant and animal records is now generally accepted” (GODWIN, 1975 : vii, echoing the words of WULFF 1943). The converse view that historically based interpretations of present day distributions must be compatible with *all* known distributional data is less widely appreciated (for discussion see WHITE, 1981, 1983b). This may be due to the fact that historical biogeography has been most conspicuously successful in north temperate countries, especially parts of Western Europe, where the flora is poor in species, and has been well-known for centuries, and where much of the contemporary chorological pattern has been shaped in response to environmental change of great magnitude (glaciation and its aftermath) during a relatively short period of time (15.000 years).

In other parts of the world, especially the tropics and subtropics, much more needs to be found out about the contemporary flora and fauna before the fruits of historical biogeography can be convincingly interpreted. It simply isn't true to say that “palaeoclimatic data are... the only means of studying ecosystem history” (DEACON & LANCASTER, 1988 : 1).

The dependence of historical biogeography on its descriptive arm, and the overwhelming importance of the latter in some parts of the world, and especially during the early stages in the development of the subject, can be traced back to the works of FORBES, DARWIN and HOOKER. The unresolved problem of the relative importance of long-distance dispersal and direct overland migration in bringing about contemporary distribution patterns has an equally long history.

FORBES (1846) had a good knowledge of European plants and animals, and of geology. He knew that the British Islands were formerly connected to the mainland of Europe and that most of Britain had been affected by the *Glacial* period which was “the epoch of glaciers and icebergs, of boulders, and groovings, and scratches”. He recognized five main elements in the British flora, which he suggested had invaded Britain at different times in response to climatic change before the land connection with Europe was severed.

FORBES explained the discontinuous distribution of one of his elements, the Arctic-alpine, on the mountain ranges of Europe as the stranded residue of a more widespread arctic flora from a period of prevalent low temperatures during the Great Ice Age which migrated across the great lowland plains of Europe. “With the rise in temperature and the retreat of the ice sheets the arctic flora was forced to ascend the mountain heights and to retreat northwards leaving behind an indication of former events in the striking discontinuity of the relict populations in disjunct mountain areas” (GODWIN, 1975 : 419).

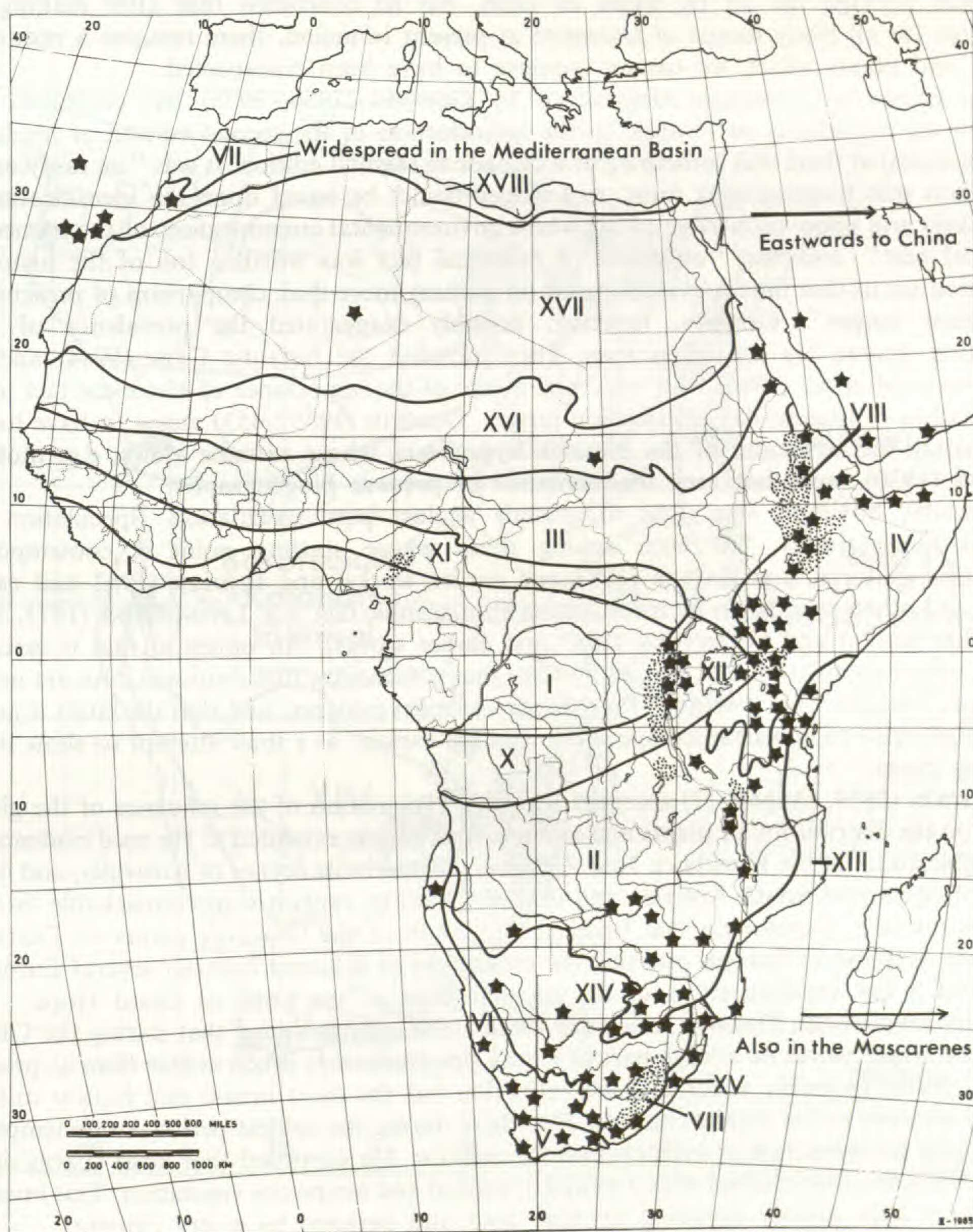


Fig. 11. — Distribution of *Olea europaea*, an African linking species (partly after GREEN & WICKENS, 1989, partly original). — NOTE : in addition to the cultivated olive, *O. europaea* subsp. *europaea* var. *europaea*, GREEN & WICKENS recognize two subspecies and one variety on the African mainland and subsp. *cerasiformis* in Macaronesia.

FORBES was well aware that some plants could have reached Britain by the conveyance of their seeds through the air by winds or birds, but he concluded that after making full allowances for all likely means of transport at present in action, there remains a residue of animals and plants which we cannot suppose to have been transported.

The Quaternary research summarized by GODWIN (1956, 1975) has confirmed and amplified the hypotheses of FORBES. In the Introduction to the second edition of his book, GODWIN says that there was something of a crusade in the first edition. It was “an essay on the proposition that biogeography must, and indeed could, be based upon the identification of plant fossils and upon knowledge of the whole environmental circumstances of the immediate geological past”, and that “an ounce of historical fact was worth a ton of the historical speculation up to that time prevalent based on nothing more than comparison of present-day distribution ranges”. GODWIN, however, possibly exaggerated the prevalence of pure speculation among his contemporaries. They included the botanist CAIN (1944) and the ornithologist MOREAU (1966) who were well aware of the importance of historical fact in the interpretation of present-day distribution ranges. GODWIN (1975 : 453) seems to have had in mind mainly the advocates of the nunatak hypothesis, whose extreme views, e.g. those of WILMOTT (1930), were not very representative of pre-war biogeography.

GODWIN, however, was right to crusade against pure speculation. Speculation still pervades biogeography, but both among those whose starting point is contemporary distribution patterns, e.g. HAFFER (1987 and earlier works) and ENDLER (1982 and earlier works), and others who begin by investigating stratigraphic fact, e.g. LIVINGSTONE (1975, 1982, and earlier works) and COLINVAUX (1987 and earlier works). An ounce of fact is certainly worth a ton of speculation, but we can now see that present-day distributional data are no less important, “weight” for “weight” than direct historical evidence, and that the latter is just as likely to give rise to unwarranted speculation as the former, as I shall attempt to show in the following pages.

DARWIN (1859, chapter 11) accepted FORBES's explanation of the influence of the glacial climate on the distribution of plants and animals, and greatly extended it. He used evidence for former glaciation (in the Himalaya, New Zealand, the southeast corner of Australia, and in the Andes of equatorial South America and central Chile) to explain some remarkable facts of plant distribution, mentioning that between 40 and 50 of the flowering plants of Tierra del Fuego are common to Europe, and that the mountains of Ethiopia harbour several European forms and a few representatives of the peculiar flora of the Cape of Good Hope.

In his own words, DARWIN concluded (with some qualifications) that during the Glacial period the whole world or a large part of it was simultaneously much colder than at present. Tropical plants probably suffered much extinction but the most humid and hottest districts afforded assylum to the tropical natives. Elsewhere during the coldest period, some temperate forms might have reached or even crossed the equator. He supposed that large spaces of the tropical lowlands were clothed with a mingled tropical and temperate vegetation. This invasion would have been greatly favoured by high land and perhaps by a dry climate.

For the tropics, some of DARWIN's ideas have recently been revived in modern dress, but not always very convincingly, e.g. refugia theory in its extreme form (e.g. DIAMOND & HAMILTON, 1980 : 398), tundra on the equator in the Lake Victoria basin (LIVINGSTONE, 1975 : 261) and ice-age aridity in tropical South America (DAMUTH & FAIRBRIDGE, 1970).

DARWIN was the first biologist to realize the world-wide importance for biogeography of

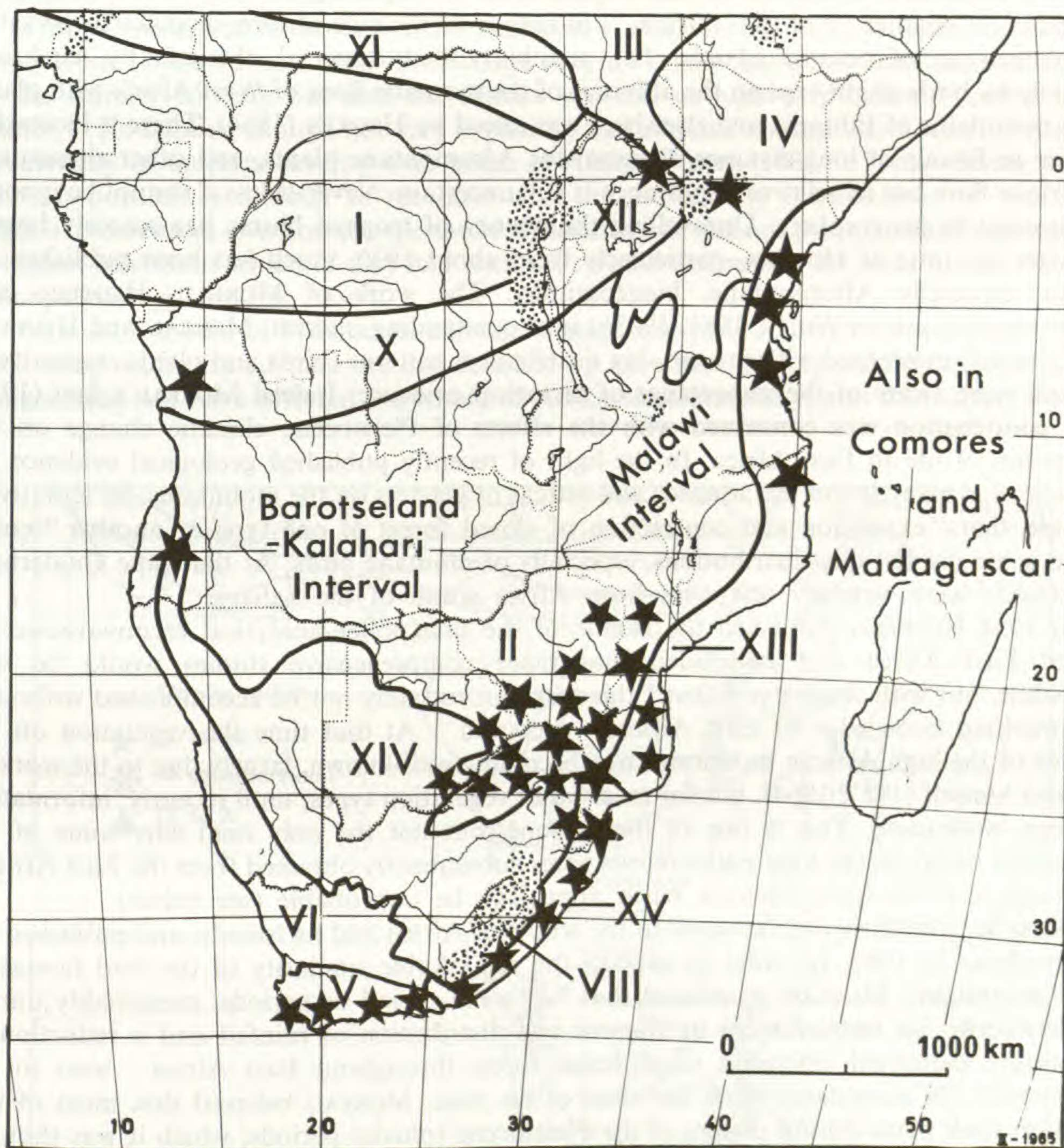


Fig. 12. — *Brachylaena*, a genus of arborescent *Compositae*. Generalized distribution of *B. huillensis* (large stars, partly after PAIVA, 1972, simplified and updated) and of the remaining African species (small stars, from various published sources). On the African mainland *Brachylaena* is an East African linking genus with outlying populations in Angola.

climatic change associated with the Glacial period. Not surprisingly, one hundred and forty years later, we now know that the picture is more complicated than he thought. In particular, he overlooked the possible importance of long-distance dispersal in enabling plants to move from one mountain to another in the tropics. This is surprising in view of his convincing arguments (in chapter 12 of the "Origin") in favour of the role of long distance dispersal in the colonization of oceanic islands. The possibility that dispersal of seeds by wind and externally by birds might explain the affinities of the montane flora of West Africa with plants on the mountains of Ethiopia and elsewhere was raised by HOOKER (1864). There is increasing evidence in favour of long-distance dispersal for Afromontane plants, and other elements in the African flora but its relative importance is still uncertain. Nevertheless it cannot be ignored by historical biogeographers. Unravelling the history of tropical biotas has scarcely begun.

After the time of HOOKER, particularly from about 1930, much has been published on African, especially Afromontane, biogeography. The work of MOREAU, HEDBERG and WICKENS (references in WHITE, 1981, 1983*b*) is of outstanding interest. MOREAU and HEDBERG were primarily concerned with present-day distribution patterns (birds and plants respectively) but both were aware of the importance of historical evidence. Indeed MOREAU's first (1933) major contribution was concerned with the effects of Pleistocene climatic change on the distribution of life in East Africa. In the light of recently published geological evidence for fluctuations in rainfall and the advance and retreat of glaciers on the mountains, he tentatively proposed that "expansion and contraction of closed forest of one type or another" could explain some present day distributions, especially of montane birds. At that time Quaternary plant fossils were virtually unknown from Africa south of the Sahara.

In 1954 HEDBERG published the results of the first pollen-analytical reconnaissance in tropical East Africa and concluded that more comprehensive studies would be well worthwhile, but with the proviso that "this task can certainly not be accomplished without a good working knowledge of East African vegetation". At that time the vegetation on the summits of the high African mountains was becoming well-known, largely due to the work of HEDBERG himself (1957, 1964), but for most other vegetation types, until recently, information has been inadequate. This is one of the reasons (but not the only one) why some of the conclusions based on the long polliniferous cores subsequently obtained from the East African mountains and the Lake Victoria basin appear to be improbable (see below).

MOREAU later extended his work to the whole of Africa and its islands, and published his final synthesis in 1966. In order to explain the remarkable similarity of the bird faunas of distant mountains, MOREAU postulated that "at some period or periods, presumably during the Pleistocene, an improvement in amount and distribution of rainfall and a reduction of temperature permitted extension of montane forest throughout East Africa... west to the Cameroons". In accordance with the ideas of his time, MOREAU believed that most of this migration took place during phases of the Pleistocene (pluvial periods, which it was thought coincided with the glacial periods of high latitudes) "when world temperature was depressed by ca. 5° C and precipitation was substantially higher than at present".

MOREAU's hypothesis has been criticized by LIVINGSTONE (1975) and others mainly on the basis of a few pollen diagrams from East Africa. LIVINGSTONE says that MOREAU's "theory must perish in the face of stratigraphic fact, for the last ice age was a time when forest trees..... were extremely scarce. At least in intramontane East Africa, the prevailing vegetation seems to have been some kind of savanna or grassland. It is still possible that — at some time too

remote to have come to our stratigraphic attention — there was a montane forest corridor across Africa, but this is not likely. We have data now for a specimen ice age and a specimen interglacial, the Holocene. Neither is characterized by widespread montane forest at low altitudes”.

The palynological evidence for the treelessness of LIVINGSTONE’s specimen ice age dates mainly from 14.700 BP to 12.000 BP. He says that low temperature was insufficient to account for the scarcity of trees but that the climate was dry enough to produce “tundra on the equator”. He implies, though not very explicitly, that climatic change was not only severe but concurrently of uniform severity over much of Africa. WHITE (1981 : 37) has shown that the aridity hypothesis is difficult to reconcile with the present-day distribution and ecology of plants like *Artemisia afra* and the species of *Dendrosenecio* without postulating changes in their ecological behaviour which, if they had occurred, would undermine the assumptions on which palaeopalynology itself is based.

MOREAU’s model of Pleistocene climatic change, except in its most extreme form, is also much more sophisticated than the one attacked by his critics. He repeatedly suggests that the changes need not have affected the whole of Africa simultaneously, and that, apart from the

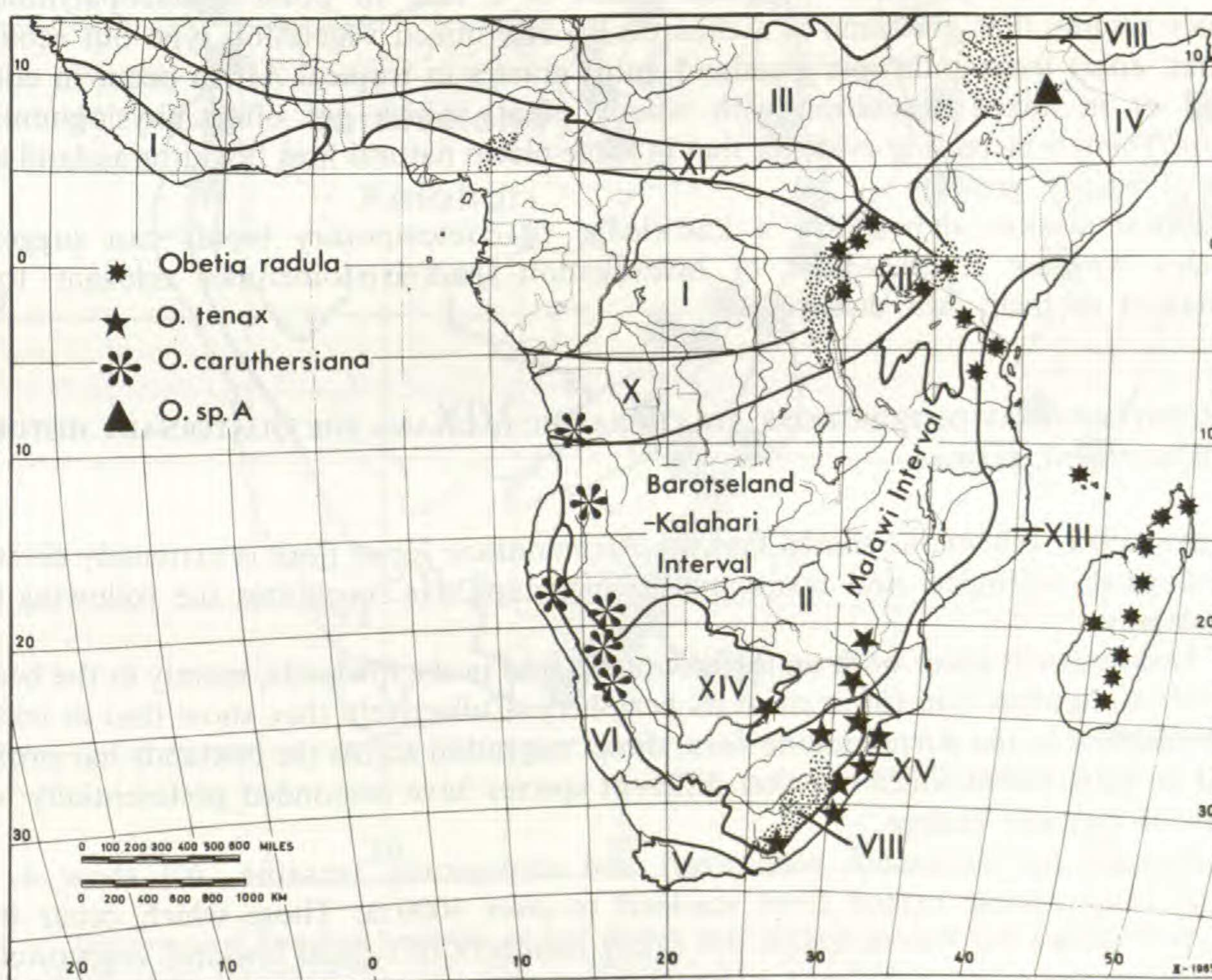


Fig. 13. — *Obetia*, a genus of arborescent *Urticaceae*. Generalized distribution of the four species occurring on the African mainland (after FRIS, 1983, map 1, simplified).

general effects, there is evidence for sub-regional fluctuations on a large scale, in some cases possibly associated with a different coastal topography and modified ocean currents. Some recent work, both on Quaternary palaeoenvironments and on present-day distributions, lends more support to MOREAU's views than to those of his critics.

Until recently, a dearth of published information on the distribution and ecology of individual plant species has seriously hindered African historical biogeography, but the situation is improving. There is now a serial "Distributiones Plantarum Africanarum" devoted to the publication of distribution maps of individual species, most of which are linked to monographic work. There is also a large scale map and a comprehensive account of African vegetation (WHITE, 1983a), and numerous more detailed local studies. Among them, LETOUZEY's publications on the flora and vegetation of Cameroun have set the highest standards. Much is now known about the Afromontane forest flora and the seed-dispersal of some of its species (DOWSETT-LEMAIRE, 1985-89; WHITE, 1981, 1983b, 1984).

In parallel with our increasing knowledge and understanding of contemporary biotas, much ingenious and painstaking work has been done in several disciplines on the Quaternary climate though some results remain equivocal. Not all authors are aware of the significance of work done in specialities other than their own, work which may cast doubt on some of their conclusions. The interpretation of grass pollen is a case in point. Palaeopalynologists sometimes assume that grassland is a climatically determined vegetation type but ecologists know that, apart from anthropic grassland, most grasses in tropical Africa occur in edaphic grassland or in mixed vegetation with woody plants which are often physiognomically dominant. There is increasing evidence that in some places natural fires favour grassland at the expense of woody growth.

The next section shows how a knowledge of contemporary biotas can suggest to Quaternary workers fruitful lines of investigation, and is sometimes relevant to the interpretation of their own discoveries.

B. CONTEMPORARY DISTRIBUTIONS, STRATIGRAPHIC FACT AND THE QUATERNARY HISTORY OF THE AFROMONTANE FLORA.

WHITE (1981, 1983b) has shown that the Afromontane forest flora is extremely diverse in its chorological, ecological and taxonomic relationships. He recognizes the following three main elements.

— *Transgressors* occur both on the mountains and in the lowlands, mainly in the heart of the Guineo-Congolian rain forest or at its periphery. Collectively they show that at least for one large element in the Afromontane flora, direct migration across the lowlands has probably occurred in quite recent times but that different species have responded preferentially to the subtleties of climatic change.

— *Nomads* are extremely widespread and ecologically versatile. All show a wide altitudinal range. Some extend from sea-level to over 3000 m. Those which occur in the "lowlands", unlike the transgressors, are rarely members of typical lowland vegetation, but are mostly confined to specialized habitats where competition is reduced such as rocky outcrops, or to especially favourable sites including the spray zone of waterfalls. Even though some species occur in Afromontane rainforest, they are all more characteristic of more open

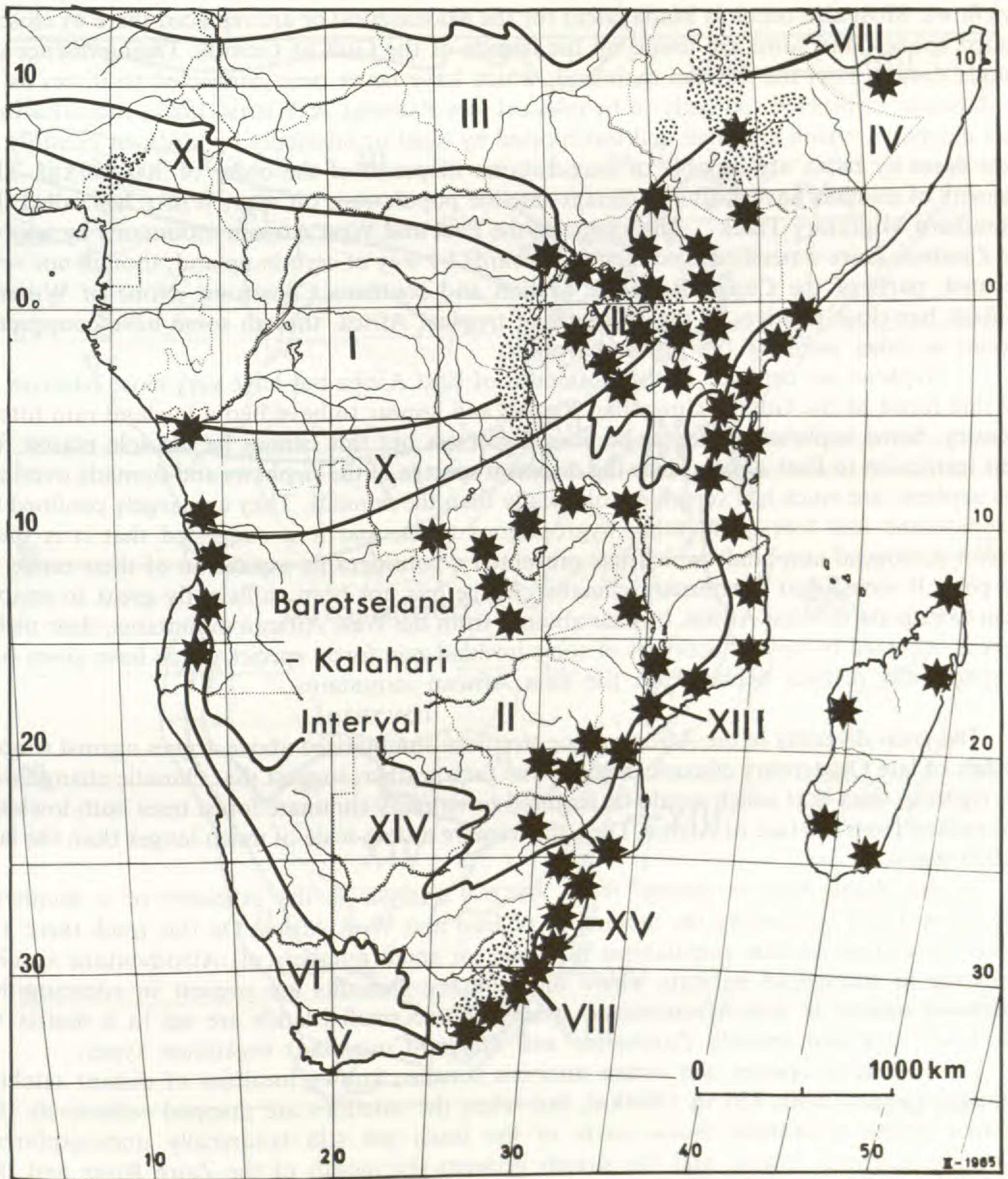


Fig. 14. — Distribution of *Strychnos henningsii*, an East African linking species with outlying populations in SW Zaire and Angola (after LEEUWENBERG, 1969, map 19, simplified and updated).

communities and all can behave as pioneers; some are fire-resistant and some can colonize lava flows. Most also occur in Madagascar (or the Mascarenes) or are replaced there by closely related species, and some are found on the islands of the Gulf of Guinea. Their presence on islands distant from the African mainland, which have never been connected to it, or, as in Madagascar, connected too early to be relevant (see PANNELL & WHITE, 1988), indicates that their diaspores, which are small and transported by wind or internally by birds (or possibly in some cases by bats), are capable of long-distance dispersal of the order of 300-800 km. The majority of nomads have scattered distant-satellite populations on what WHITE has called the "Southern Migratory Track". This connects the East and West African mountains by way of the Zambezi-Zaire watershed, and then northwards by way of certain upland, though not very elevated, parts of the Congo Republic, Gabon and southern Cameroun. None of WHITE's nomads has close relatives in the lowlands of tropical Africa, though some have congeneric species in other parts of the lowland tropics.

— *Nephews* are confined to the mountains of East Africa but have very close relatives in the rain forest of the Guineo-Congolian Region and appear to have had a lowland rain forest ancestry. Some nephews appear to be poor dispersers but this cannot be the sole reason for their restriction to East Africa, since the dispersal spectra of the nephews and nomads overlap. The nephews are much less versatile ecologically than the nomads. They are largely confined to Afromontane rain forest and other hygrophilous types, and it is suggested that it is their narrow ecological amplitude which has prevented a considerable expansion of their range in the past. It seems that Quaternary climatic change has not been sufficiently great to enable them to migrate to West Africa. In their absence from the West African mountains, their niche there is occupied by upland ecotypes of some lowland rain forest species which have given rise to specifically distinct nephews on the East African mountains.

The great diversity of the Afromontane tree flora summarized above argues against simple models of late Quaternary climatic change. The facts, rather, suggest that climatic change was less rigorous than that which would be required to virtually eliminate forest trees both lowland and upland from the face of Africa. They also require a time-scale of much longer than the last 20,000 years.

A remarkable fact to emerge from WHITE's analysis is the existence of a Southern Migratory Track connecting the mountains of East and West Africa. On this track there are numerous distant satellite populations of single (or small numbers of) Afromontane species occurring in specialized habitats where the montane elements are present in communities composed mainly of non-Afromontane species. These small islands are set in a matrix of "lowland" regional (mainly Zambezian and Guineo-Congolian) vegetation types.

For individual species, the widest intervals between known localities of distant satellite populations vary from 850 to 1500 km, but when the satellites are mapped collectively the distance drops to 300 km. Some parts of the track are still botanically underexplored, especially northern Angola and the stretch between the mouth of the Zaire River and the Cameroun highlands. Further exploration is likely to show that the distant satellite populations are more numerous and closer together than they appear to be at present. Their insignificant size, however, in relation to the surrounding vegetation is firmly established.

In view of the known vagility and ecological versatility of the nomads, it is tempting to suppose that they have travelled across Africa under something like contemporary climatic

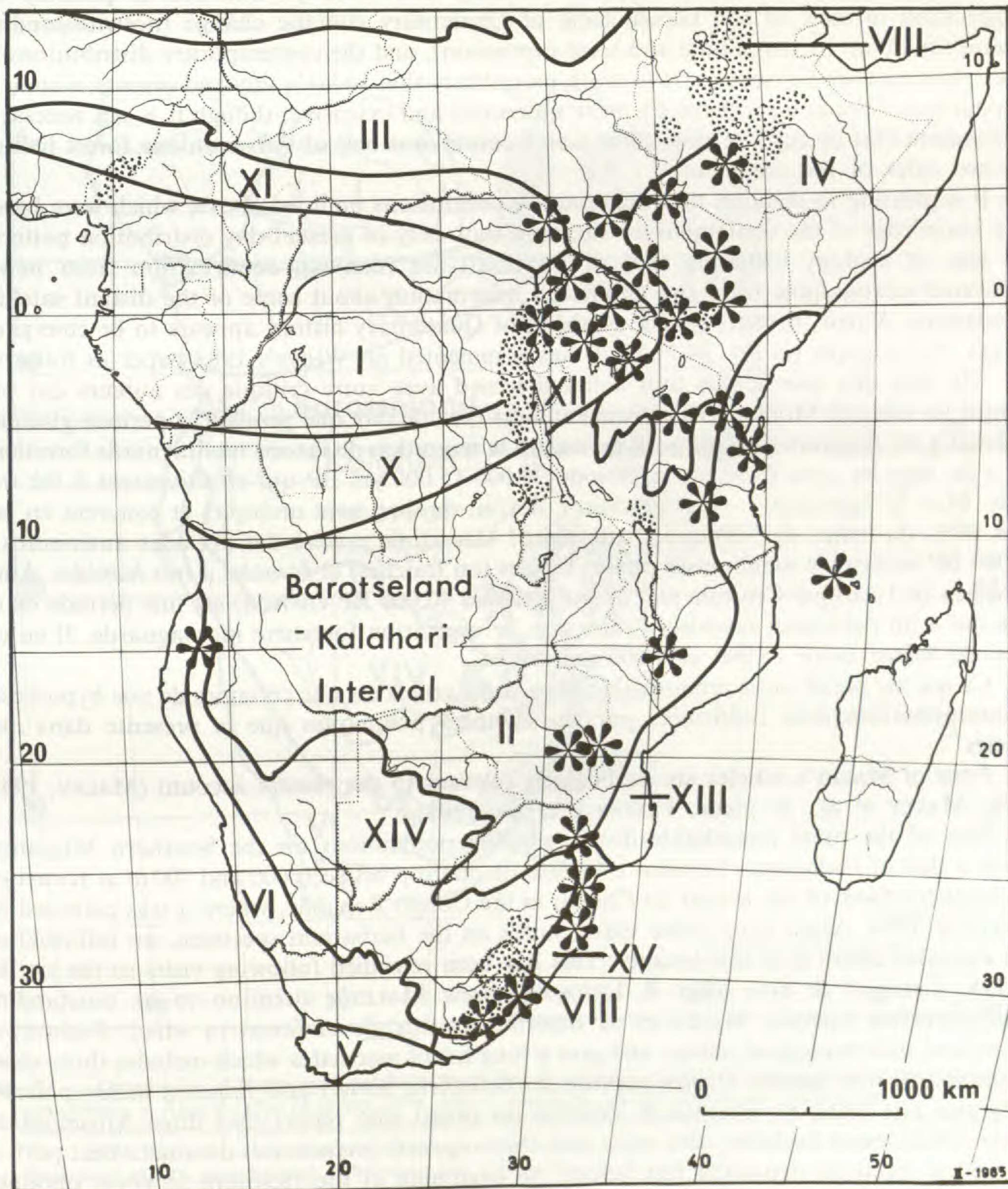


Fig. 15. — Distribution of *Strychnos mitis*, an East African linking species with outlying populations in Angola (after LEEUWENBERG, 1969, map 30, simplified and updated).

conditions, and that (*contra* LIVINGSTONE) what is in effect (in terms of migrational opportunity) a montane forest corridor actually exists today. But this is possibly an exaggeration in view of the known facts of Quaternary climatic change (notwithstanding uncertainty about its magnitude and local expression), and the contemporary distributions of other plant and animal species. It is much more likely that today's tiny and remote islands of Afromontane species were formerly more numerous and extensive, though it is not necessary to postulate that at any one time there was a continuous belt of Afromontane forest linking the two sides of the continent.

It is pleasing to mention that the tentative conclusions outlined above, which were based on a knowledge of the contemporary situation (not only of present-day distribution patterns but also of ecology including that of dispersal) are receiving confirmation from newly discovered stratigraphic facts and additional information about some of the distant satellite populations. A new, broadly based, synthesis of Quaternary history appears to be emerging. MALEY, for example (*in litt.* 24.11.1989) has commented on WHITE's 1983 paper as follows :

“Je dois dire que je suis tout à fait d'accord avec votre critique des auteurs qui ont attaqué les idées de MOREAU. Effectivement il est faux de dire que pendant la période glaciaire le climat a été toujours trop sec pour permettre la migration de taxons montagnards forestiers. On a eu trop les yeux fixés sur la période 20.000-15.000 yrs BP qui effectivement a été très aride. Mais le “glaciaire” — les glaciaires, devrait-on dire, sont multiples et couvrent en fait 80 à 90 % du temps de l'époque Quaternaire ! Une étude précise des périodes antérieures à 20.000 BP montre de nombreuses phases froides (ou fraîches) et *humides à très humides*. Ainsi le Njilien de l'Afrique Centrale (ca. 27 ou 30.000 à 40.000 BP environ) est une période de ce type qui a dû nettement favoriser l'extension de végétation forestière montagnarde. Il en est aussi de même entre 15.000 et 9.000 ans BP.

Ce qui me paraît aussi remarquable dans votre article est que certaines de vos hypothèses et interprétations sont confirmées par des données polliniques que je présente dans mes articles”.

Four of MALEY's articles are particularly relevant to the present account (MALEY, 1987, 1989; MALEY et al., in press; FRÉDOUX et al., 1989).

One of the most remarkable distant-satellite populations on the Southern Migratory Track is that of *Podocarpus latifolius* on a laterite outcrop between 600 and 700 m at Kouyi on the southern flank of the massif du Chaillu in the Congo Republic, where it was collected by P. SITA in 1974. Apart from some sparse notes on the herbarium specimen, no information was available about it at this locality. This has been remedied following visits to the site by MALEY, CABALLÉ & SITA after R. LETOUZEY drew MALEY's attention to its outstanding biogeographical interest. MALEY et al. describe the islands of forest in which *Podocarpus* occurs and their ecological milieu, and give a long list of associates which includes three other Afromontane tree species, *Ocotea gabonensis*, *Schefflera barteri* and *Rapanea melanophloeos*. They also cite work by ELENGA & VINCENS (in press) who report that three Afromontane species *Podocarpus latifolius*, *Ilex mitis* and *Olea capensis* (*welwitschii*) dominate that part of the pollen spectrum deposited just before the beginning of the Holocene in cores obtained from a small depression at about 600 m in altitude on the Batéké Plateau north of Brazzaville and 300 km distant from Kouyi.

Podocarpus latifolius is also the subject of a preliminary note by FRÉDOUX et al. They record the occurrence of its pollen grains in a marine core from the Gulf of Guinea 125 km

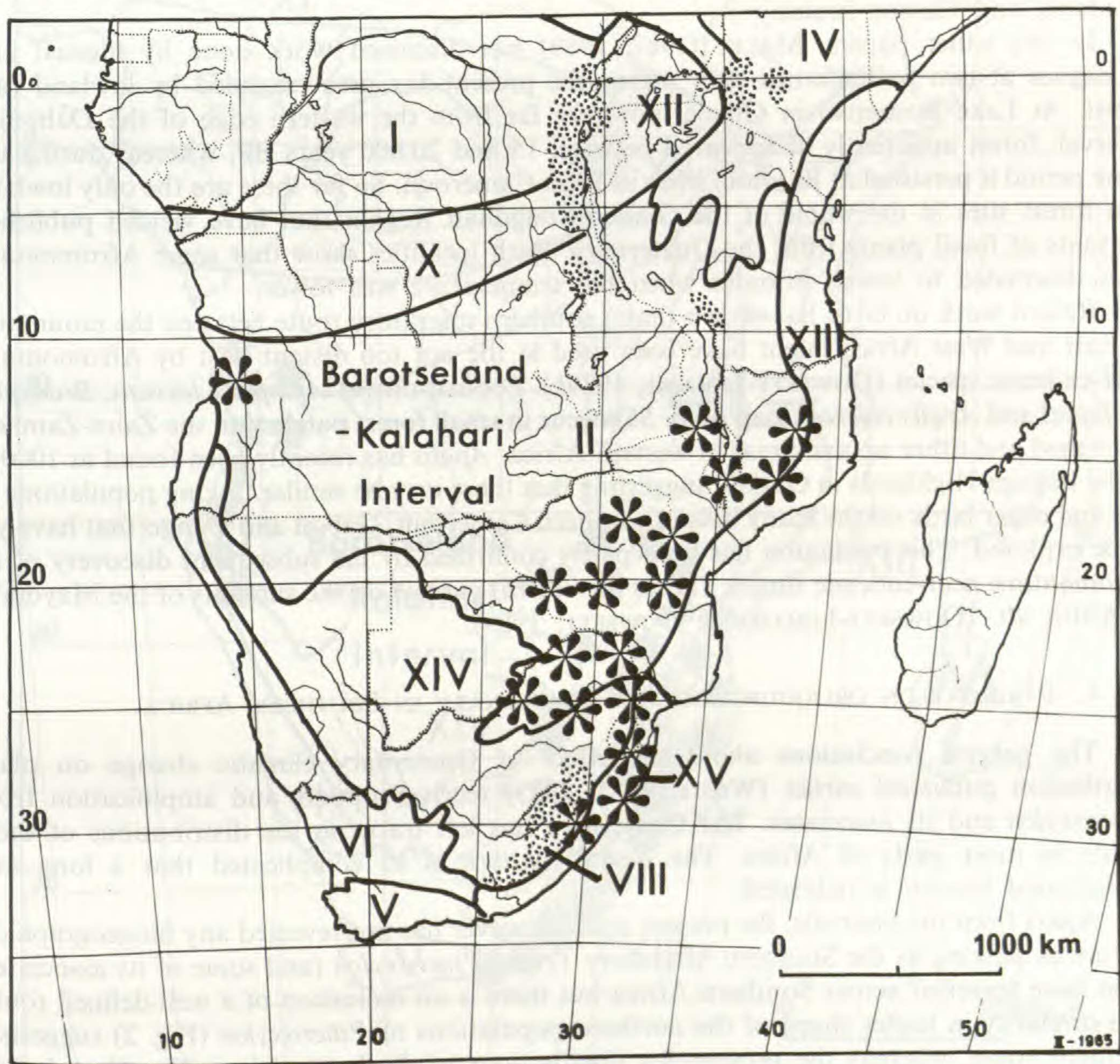


Fig. 16. — Distribution of *Heteropyxis natalensis* (including *H. dehniae*), an East African linking species with outlying populations in Angola (after MARTINS, 1976, map 1, simplified, and information in FERNANDES, 1971). — NOTE : *Heteropyxis* is the only genus in the African endemic family *Heteropyxidaceae* (see VAN WYK in DAHLGREN & VAN WYK, 1988). The only other species of *Heteropyxis*, *H. canescens*, is confined to the south-eastern Transvaal and Swaziland and its geographical distribution lies within that of *H. natalensis*

south of Abidjan. It was present throughout the isotopic stages 6 to 4 (50.000 to 150.000 BP) and was relatively abundant during the colder phases 5d and 5b. From this, they infer that *P. latifolius* was present, at that time, in the Upper Guinea highlands (where it doesn't occur today) and during the coldest phases descended to lower altitudes at several places in the Bandama and Comoe basins.

In two other papers, MALEY (1987, 1989) has discussed work done by himself and colleagues at two polliniferous sites within the present-day area occupied by lowland rain forest. At Lake Bosumtwi in Ghana, not very far from the western edge of the Dahomey Interval, forest apparently disappeared between 15 and 20.000 years BP, whereas during the same period it persisted at Barombi Mbo in West Cameroun. So far these are the only lowland rain forest sites in the whole of the Guineo-Congolian Region that have yielded published accounts of fossil plants from the Quaternary. Both localities show that some Afromontane trees descended to lower altitudes when the temperature was lower.

Recent work on birds has shown that a southern migratory route between the mountains of East and West Africa might have been used in the not too distant past by Afromontane near-endemic species (DOWSETT-LEMAIRE, 1989b). Populations of *Aplopelia larvata*, *Bradypterus lopezi* and *Apalis cinerea* (map on p. 55) occur in small forest patches on the Zaire-Zambezi watershed and other upland areas in western Africa. *Apalis* has recently been found at 1000 m in the Belinga Highlands in Gabon, suggesting that there may be similar linking populations of this and other birds on the many hills of southern Cameroun, Gabon and Congo that have yet to be explored. This prediction has been partly confirmed by the subsequent discovery of an Afromontane near-endemic thrush *Turdus (Zoothera) gurneyi* on the summits of the Mayombe at 550 m alt. (DOWSETT-LEMAIRE & DOWSETT, 1989).

C. PTAEROXYLON OBLIQUUM AND THE QUATERNARY IN SOUTHERN AFRICA.

The general conclusions about the effect of Quaternary climatic change on plant distribution published earlier (WHITE, 1981, 1983) receive support and amplification from *Ptaeroxylon* and its associates. The Quaternary has left traces in the distributions of these plants in most parts of Africa. The overall pattern is so complicated that a long and complicated history is indicated.

Apart from the intervals, the present study however has not revealed any biogeographical feature as striking as the Southern Migratory Track. *Ptaeroxylon* (and some of its associates) must have travelled across Southern Africa but there is no indication of a well-defined route. The similarity in leaflet shape of the northern populations of *Ptaeroxylon* (Fig. 2) suggests a northern route, whereas the present-day distributions of *Euclea undulata* (Fig. 6) and *Olea europaea* (Fig. 11) show that a southern route might have been possible. *Euclea divinorum* indicates (Fig. 6) a middle one at about the latitude of the Zambezi. Different species might have gone by different ways, possibly at different times or migration was possibly diffuse.

Evidence for Late Quaternary climatic change in Southern Africa (south of the Zambezi) has been recently synthesized by DEACON & LANCASTER (1988) but it is difficult to relate this information to the distribution patterns of the contemporary flora.

According to DEACON & LANCASTER, "the main aim of palaeoclimatic research is to describe variations in climate in the period beyond the range of the meteorological record. The ultimate goal is theoretical : to understand the physical causes of these variations". Among

the primary data from which climatic conditions can be inferred, they include (p. 2) floral analyses that are accurately located in time and space, usually by being within a well-dated sequences of sediments. But they have little to say about the reciprocal role of palaeoclimatology and biogeography.

Unfortunately, available primary palaeobotanical data for Southern Africa are sparse and, at present, difficult to interpret. "There are few large sedimentary basins and little opportunity for the accumulation of organic-rich sediments" (p. 29). "More precise data are needed on the distribution patterns of modern plants and animals, and the degree to which they can tolerate changes in environmental parameters" (p. 163). Local phytochorological studies of the flora surrounding polliniferous sites such as Wonderkrater in the Transvaal are also needed before drawing detailed climatic inferences (p. 171).

Historical biogeography in Southern Africa has a long way to go. It might be rewarding if palaeobotanists were to make a deliberate search for fossil remains of plants like *Ptaeroxylon* which are easy to identify and pose striking historical problems. The structure of the pollen grains and secondary xylem of *Ptaeroxylon* is so distinct that it supports the elevation of *Ptaeroxylon* to family rank. Fossil leaves and fruits should also be easy to identify since they are unlike those of any other African plant.

It is possible that the future discovery of fossils of *Ptaeroxylon* from localities outside its present distribution would contribute as much to our understanding of past climatic change as would the analysis of long polliniferous cores. Such discoveries would be comparable in interest to those made by MALEY for *Podocarpus* (see above), and by BONNEFILLE & LETOUZEY (1976) for fossil *Antrocaryon* in Ethiopia far distant from its nearest known contemporary occurrences.

CONCLUSIONS

Since the end of the second world war, in other words during the professional life of René LETOUZEY, our knowledge (ecological, chorological and taxonomic) of African vegetation has grown apace, though much remains to be discovered.

During the same period there have been great advances in our understanding of the African Quaternary, though the precise interpretation of the facts is often equivocal.

To a certain extent, studies of these major divisions of biogeography — descriptive and historical — have been out of phase, in that information about the past has sometimes been obtained before the present was fully understood. It has not always been realized by historical biogeographers that explanations of the present in terms of the past must be based on an intimate knowledge of the former. This is especially so with regard to the grass component in pollen diagrams.

There are welcome signs, however, that a new synthesis may be emerging. Some Quaternary workers (e.g. DEACON & LANCASTER) acknowledge the inadequacy of the currently available palaeobotanical record, and others (e.g. MALEY) have recently combined studies of contemporary vegetation with their interpretations of the stratigraphic record.

The time has come when botanists who study contemporary patterns should assert the central role of their work in historical biogeography. There is room for more active co-operation between them and those whose interest is more exclusively focussed on the past.

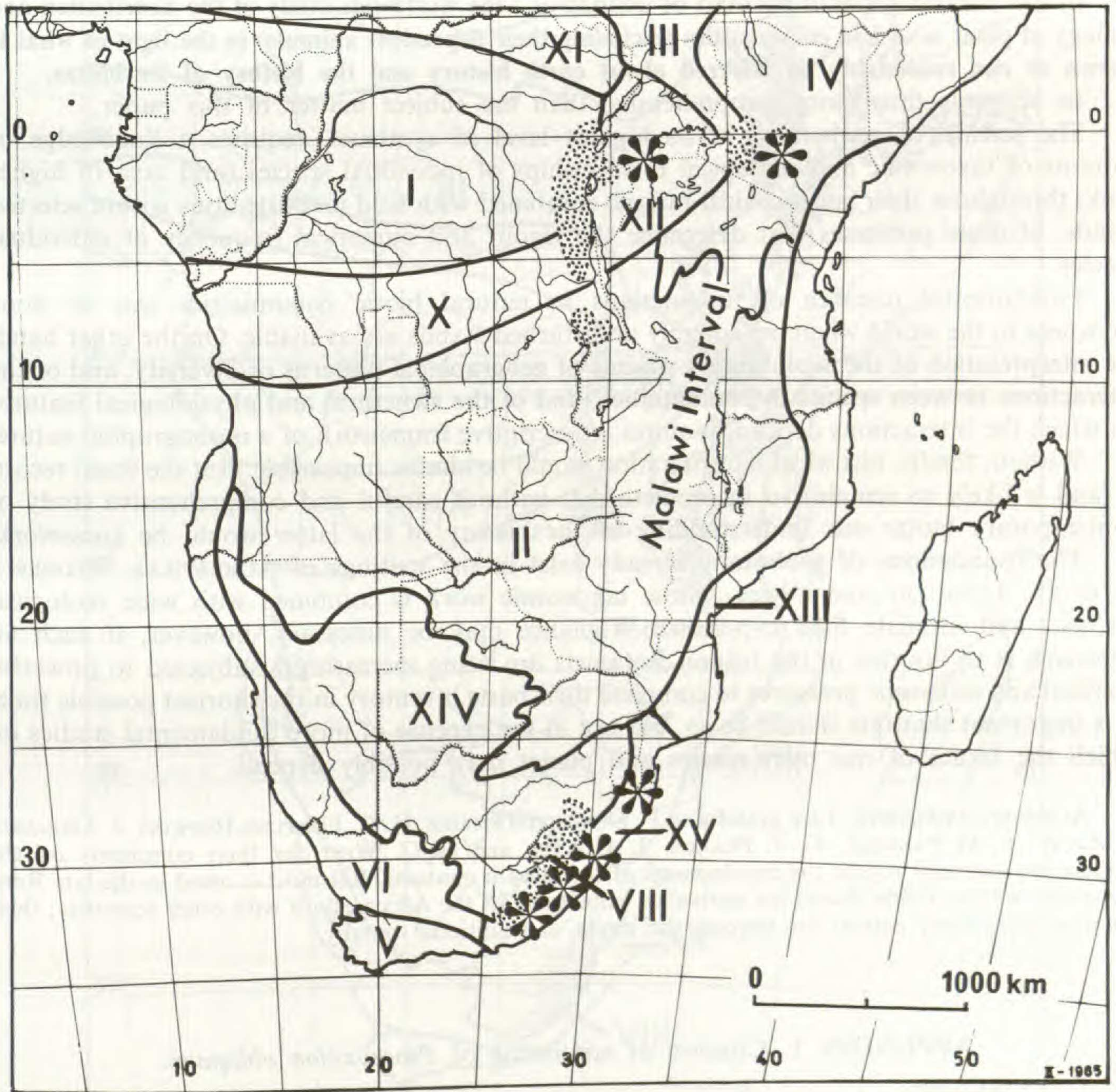


Fig. 18. — Generalized distribution of *Heywoodia lucens*, an East African linking species showing a greatly enlarged Malawi Interval (after MILNE-REDHEAD, 1957, fig. 32, simplified and updated).

Synthesis of this kind involving the results of the various specialities within biogeography might best be achieved within the framework of a revitalized and expanded science of **GEOBOTANY**.

In this context geobotany could be defined as : **the worldwide study of the distribution and ecology of plant taxa and communities (including their dependent animals) in the light of what is known or can reasonably be inferred about earth history and the history of its biotas.**

Its scope is thus more comprehensive than the subject matter of this paper.

The science of geobotany, at its highest level of synthesis, requires a knowledge of patterns of taxonomic and ecological relationships of individual species (and taxa of higher rank) throughout their geographical ranges, combined with field investigations within selected stands, of those processes that determine the vigour and numerical frequency of individual species.

Fundamental research on interactions in natural biotic communities can be done anywhere in the world where reasonably undisturbed stands are available. On the other hand, the interpretation of the evolutionary origins of geographical patterns of diversity, and of the interactions between species in communities, and of the structural and physiological features on which the interactions depend, requires a descriptive framework of a monographic nature.

Without fossils, historical interpretation would be almost impossible. But the fossil record is (and is likely to remain) so incomplete that without careful and comprehensive study of contemporary biotas our understanding of the history of the latter would be guesswork.

The foundations of geobotany already exist in the writings of AUBRÉVILLE, HEDBERG, LÉONARD, LETOUZEY and others, whose taxonomic work is combined with wide biological interests and intimate field experience. Vigilance may be necessary, however, if such an approach is to flourish in the future. Botanists are being increasingly subjected to powerful political and economic pressures to complete their basic inventory in the shortest possible time. It is important that this should be so, but not at the expense of more fundamental studies on which the future of our own species and planet may possibly depend.

ACKNOWLEDGEMENTS : I am grateful to F. DOWSETT-LEMAIRE, H. C. FORTUNE-HOPKINS, J. LÉONARD, J. MALEY, C. M. PANNELL, G. T. PRANCE, J. A. WEBB and R. G. WEST for their comments on the manuscript and their role in the development of the ideas it contains. But most is owed to the late René LETOUZEY who so freely shared his unrivalled knowledge of the African flora with other scientists; their interests collectively extend far beyond the limits of traditional botany.

APPENDIX 1. Citation of specimens of *Ptaeroxylon obliquum*.

One herbarium specimen (examined by me) is cited for each one-degree square in which the species is known to occur. For four additional degree squares the information given is based on my own field observations.

TANZANIA. — SE 0438 : West Usambara Mts., Sunga-Manolo, 1950 m, *Drummond & Hemsley* 2774 (K).

MOZAMBIQUE. — SE 2632 : Santaca, *Gomes e Sousa* 3869 (PRE, SRGH).

ZIMBABWE. — SE 2028 : Matopos Hills, Besna Kobila, *White* 10067 (FHO). — SE 2031 : Ndanga Distr., Mutewe R., *Savory* 501 (SRGH).

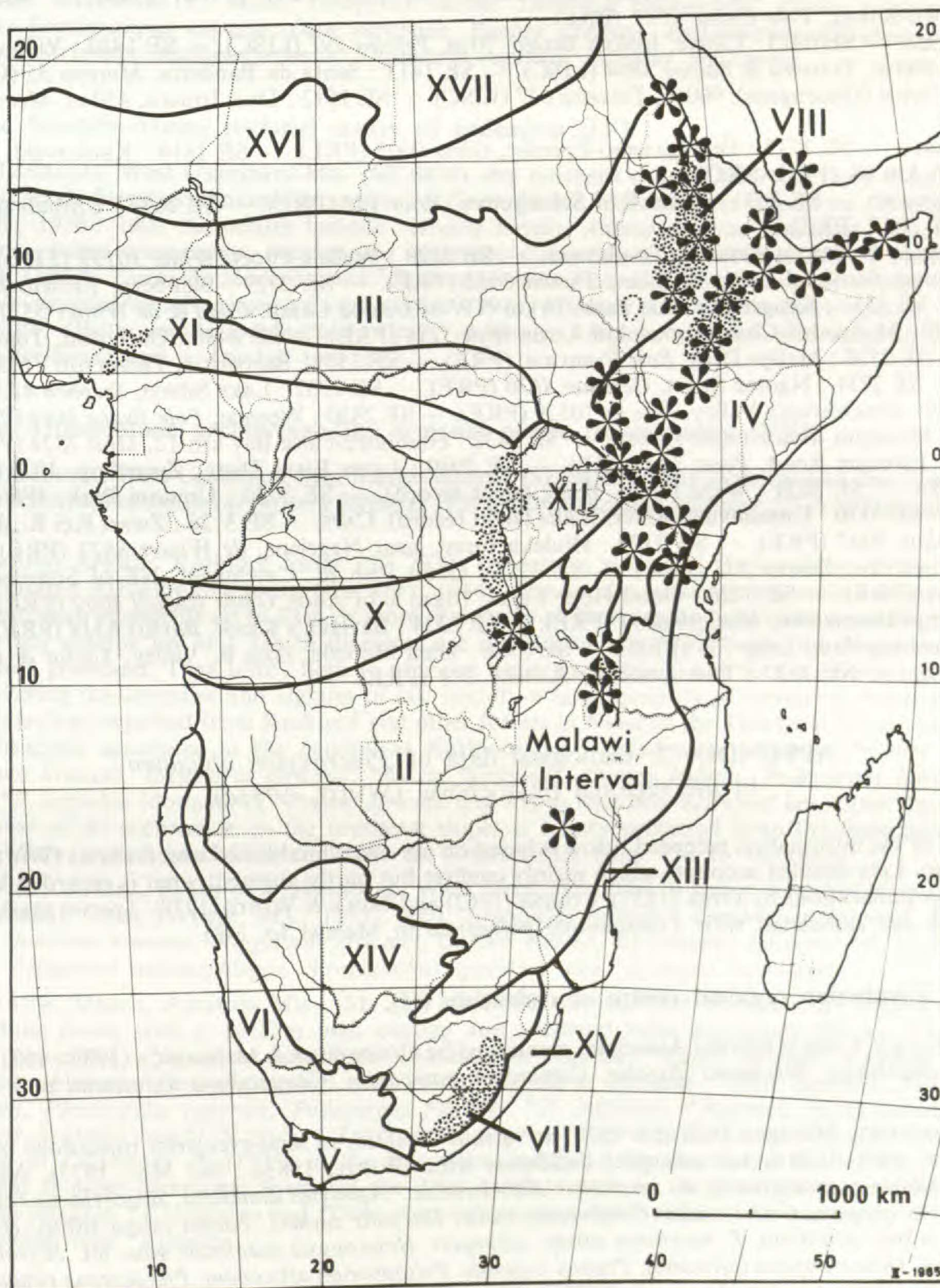


Fig. 19. — Generalized distribution of *Juniperus procera*, an Afromontane endemic species (based mainly on materials assembled for WHITE, 1983a). — NOTE : related species occur in the eastern Mediterranean basin and eastwards to the Himalayas (see KERFOOT & LAVRANOS, 1984).

BOTSWANA. — SE 2027 : Sebina-Kalamakati, *Pole-Evans* 3264 (FHO, PRE). — SE 2127 : Francistown-Bosoti, *Pole-Evans* 3237 (PRE).

ANGOLA. — SE 0913 : Catete, Icolo e Bengo, 70 m, *Pereira* 297 (LISC). — SE 1412 : Villa Arriaga, Montipa, 800 m, *Teixeira & Santos* 3864 (LISC). — SE 1413 : Santa da Bandeira, *Moreno* 35 (COI). — SE 1414 : Senje (Quilengues), 900 m, *Teixeira* 627 (LISC). — SE 1512 : Dois Irmaos, 450 m, *Mendes* 3885 (LISC).

NAMIBIA. — SE 1713 : Otjansasemo-Epembe, *Giess* 9003 (PRE). — SE 1814 : Kaokoveld, Ohopokamanjab km 88 (PRE, SRGH).

SWAZILAND. — SE 2631 : 16 km S of Sidvokodvo, *Prior* 131 (PRE). — SE 2632 : Umbuluzi Gorge, *Culverwell* 1057 (PRE).

REPUBLIC OF SOUTH AFRICA : TRANSVAAL. — SE 2229 : Wylie's Poort, *White* 10159 (FHO). — SE 2231 : Kruger National Park, Wambia, *Theron* 2612 (PRE). — SE 2329 : Blaauwburg, *Tscheuschner* s.n. (PRE). — SE 2331 : Kruger National Park, 24 km NW of Letaba Camp, *Codd & de Winter* 5571 (PRE). — SE 2429 : Malipsdrif-Chuniespoort km 4, *van Wyk* 5236 (PRE). — SE 2430 : Ohrigstad, *Young* A722 (PRE). — SE 2530 : Malips Drift, *Pole Evans* s.n. (PRE). — SE 2531 : Barberton, *Thorncroft* 1115 (PRE). NATAL. — SE 2731 : Ngome forest, *Gerstner* 4870 (PRE). — SE 2732 : Lake Sibayi, *Stephen* 412 (PRE). — SE 2829 : Blaauwkrantz Valley, *Acocks* 10529 (PRE). — SE 2830 : Weenen, *Pole Evans* 3819 (PRE). — SE 2831 : Mtunzini, *White* (sight record). — SE 2832 : Hluhluwe-False Bay km 12, *Moll* 2824 (PRE). — SE 2929 : Estcourt Road, *Pentz* 544 (PRE). — SE 2930 : Lions River Distr., Zwartkop, 1370 m, *Moll* 1150 (PRE). — SE 3029 : Weza forest, *White* (sight record). — SE 3030 : Umdoni Park, *White* (sight record). — SE 3130 : Umtamvuna River, *White* (sight record). CAPE. — SE 3126 : Zwart Kei R., Junction Farm, *Galpin* 8097 (PRE). — SE 3129 : Hluleka forest, near Ngqelene, *de Winter* 8827 (PRE). — SE 3224 : Jansenville, *Theron* 235 (PRE). — SE 3225 : Great Fish R., Catchment, NE of Somerset East, *Jenkins* s.n. (PRE). — SE 3226 : Good Hope Farm, 10 km E of Alice, *Gibbs Russell* 4002 (PRE). — SE 3227 : Kingwilliamstown, *Marloth* 6031 (PRE). — SE 3324 : Baviana's Kloof, *Bayliss* 6314 (PRE). — SE 3325 : Zuurberg Pass, *Long* 706 (PRE). — SE 3326 : Glen Melville, Ecce R. Valley, *Taylor & Edwards* 8785 (PRE). — SE 3327 : East London, *Rattray* 278 (PRE).

APPENDIX 2. Ecological data of *Ptaeroxylon obliquum* in the regional phytochoria (WHITE, 1983a).

Most of the information recorded below is based on my own unpublished observations (WHITE, MS., 1973, 1976). Less detailed accounts which mainly confirm but partly augment what is recorded here can be found in publications by DYER (1937), COMINS (1962) and MOLL & WHITE (1978). Species marked with an asterisk are associated with *Ternstroemia polypetala* in Malawi (p. 148).

The Zambezian regional centre of endemism (II).

1. ANGOLA, Little is known. Associates mentioned by GOSSWEILER & MENDONÇA (1939 : 152) include *Balanites angolensis*, *Berchemia discolor*, *Combretum camporum*, *Commiphora welwitschii* and *Maerua angolensis*.

2. ZIMBABWE, Matopos Hills (SE 2028) at various localities in semi-evergreen rupicolous bushland and thicket with 10-20 m tall emergent deciduous trees (WHITE, 1983a : 98; MS., 1973). Associates include : *Albizia tanganyicensis*, *A. versicolor*, *Aloe excelsa*, **Apodytes dimidiata*, *Brachylaena rotundata*, *Calodendrum capense*, *Catha edulis*, *Combretum molle*, *Dovyalis zeyheri*, *Euclea crispa* subsp. *crispa*, *E. natalensis* subsp. *acutifolia*, *E. racemosa* subsp. *schimperi*, *Heteropyxis natalensis* sens. lat. *Myrothamnus flabellifolius*, *Olea europaea* (africana), *Pappea capensis*, *Peltophorum africanum*, *Pterocarpus rotundifolius*, *Steganotaenia araliacea*, *Strychnos usambarensis*, *Turraea fischeri*, *T. floribunda*, *Zanthoxylum capense* and succulent tree *Euphorbias*.

3. TRANSVAAL, Wylie's Poort, Soutpansberg (SE 2229), 610 m, in semi-evergreen rupicolous bushland with scattered evergreen and deciduous emergent trees 8-12 m tall (WHITE 1983a : 98; MS., 1973 : 93). Associates include : *Acacia ataxacantha*, *A. nigrescens*, *Albizia amara*, *Calodendrum capense*,

Combretum hereroense, *C. molle*, *Diospyros villosa*, *Dombeya rotundifolia*, *Euclea racemosa* subsp. *zuluensis*, *Lonchocarpus capassa*, *Olea europaea*, *Pappea capensis*, *Peltophorum africanum*, *Pteleopsis myrtifolia*, *Strychnos madagascariensis*, *Tecomaria capensis*, *Ziziphus mucronata*.

The Somalia-Masai regional centre of endemism (IV).

4. TANZANIA, West Usambara Mts. (SE 0438), dry northern slopes, 700-960 m, in 9-15 m tall semi-evergreen scrub forest dominated by species of *Commiphora* and succulent *Euphorbia* (WHITE, 1983a : 117; MS., 1976 : 140). Associates include : *Acacia tortilis*, *Adenia globosa*, *Adenium obesum*, *Azelia quanzensis*, *Azima tetracantha*, *Brachylaena huillensis*, *Commiphora* spp. (White 11927, 11932, 11939, 11940 & 11942), *Cussonia zimmermannii*, *Dalbergia melanoxylon*, *Euclea racemosa* subsp. *schimperii*, *Euphorbia candelabrum*, *E. cooperi*, *E. spp.* (White 11945, 11946 & 11947), *Manilkara sulcata*, *Newtonia hildebrandtii*, *Obetia radula* (pinnatifida), *Opilia campestris*, *Pappea capensis*, *Scorodophloeos fischeri*, *Turraea floribunda* and a 4 m tall tree *Aloe*.

The Afromontane archipelago-like regional centre of endemism (VIII).

5. TANZANIA, West Usambara Mts. Sunga-Manolo (SE 0438); apart from the fact that it occurs (or formerly occurred) in *Juniperus procera* forest at 1950 m (Drummond & Hemsley 2774) nothing apparently is known.

6. SOUTH AFRICA, Karkloof forest (SE 2930) on eastern slopes of Drakensberg, 1220-1525 m in undifferentiated Afromontane forest (RYCROFT, 1944). *Ptaeroxylon* occurs in the main canopy which is 18-24 m tall with emergents up to 27 m or more. Few trees of *Ptaeroxylon* have boles more than 60 cm in diameter but stumps up to 1.3 m in diameter are not uncommon both inside the forest and in the surrounding grassland. They testify both to previous heavy exploitation and to the destruction of forest by fire. During the seventies and eighties of last century a large quantity of timber of *Ptaeroxylon* and other species was exported from Karkloof and other forests in Natal to the Transvaal for use in the gold mines. Principal associates in the canopy at Karkloof are : *Calodendrum capense*, **Celtis africana*, *Combretum kraussii*, *Kiggelaria africana*, **Nuxia floribunda*, *Ocotea bullata*, *Podocarpus falcatus*, **P. henkelii*, **P. latifolius* (dominant), **Prunus africana* and *Vepris undulata*. Karkloof lies within the mist-belt and because of its occurrence on the southeast slopes is largely protected from the desiccating "berg winds". Mean annual rainfall in and near the forest varies from 750 to 1875 mm.

7. SOUTH AFRICA, flanks of Drakensberg; Weza forest (SE 3029) in rather disturbed 30 m tall forest with abundant *Usnea* (WHITE, MS., 1973 : 300). Associates include : *Combretum kraussii*, *Dalbergia obovata*, *Gonioma kamassi*, *Kiggelaria africana*, *Ocotea bullata*, *Podocarpus falcatus*, **P. henkelii*, **P. latifolius*, **Rapanea melanophloeos*, *Strophanthus speciosus* and **Xymalos monospora*.

8. SOUTH AFRICA, Amatola Mts., (SE 3227) 765-1350 m, very rare in rather dry undifferentiated Afromontane forest with a 16-22 m high canopy and scattered taller emergents (STORY, 1952 : 68). Principal associates : **Apodytes dimidiata*, *Calodendrum capense*, **Celtis africana*, *Curtisia faginea*, **Diospyros whyteana*, *Dovyalis zeyheri*, *Ilex mitis*, *Kiggelaria africana*, **Olea capensis*, *Pittosporum viridiflorum*, *Pleurostyliia capensis*, *Podocarpus falcatus*, **P. latifolius*, **Rapanea melanophloeos*, *Rhus chirindensis*, *Scolopia mundii*, *S. zeyheri*, *Trichocladus ellipticus*, *Vepris undulata* and **Xymalos monospora*. According to CHALK et al. (1935) in the mountain forests of the Amatolas and of the Transkei, *Ptaeroxylon* is more commonly found in the drier habitats such as rocky ridges in association with *Podocarpus falcatus*, **P. latifolius* and **Olea capensis* than in moister places characterized by *P. henkelii*, *Ocotea bullata* and **Xymalos*.

The Kalahari-Highveld regional transition zone (XIV). See p. 144.

The Tongaland-Pondoland regional mosaic (XV).

9. SOUTH AFRICA, Ndumu to Maputa km 23 (SE 2632), in 18 m tall "sand" forest (MOLL, 1968; MOLL & WHITE, 1978 : 582; WHITE, 1983a : 199; MS., 1973 : 215). Associates include : *Azelia*

quanzensis, *Albizia forbesii*, *Balanites maughamii*, *Berchemia discolor*, *Cassine transvaalensis*, *Cleistanthus schlechteri*, *Combretum molle*, *Dialium schlechteri*, *Erythrophleum lasianthum*, *Euclea natalensis* subsp. *natalensis*, *Euphorbia grandicornis*, *Galpinia transvaalica*, *Hymenocardia ulmoides*, *Newtonia hildebrandtii*, *Podocarpus falcatus*, *Pteleopsis myrtifolia*, *Schotia brachypetala*, *Sclerocarya caffra*, *Spirostachys africana*, *Strychnos decussata*.

10. SOUTH AFRICA, near Maputa (SE 2632), 50 m alt., in 22 m tall undifferentiated forest (WHITE, 1983a : 199; MS., 1973 : 220). Associates include : *Albizia adianthifolia*, *Balanites maughamii*, **Celtis africana*, *Chaetacme aristata*, *Chrysophyllum viridifolium*, *Combretum kraussii*, *Croton sylvaticus*, *Dialium schlechteri*, *Diospyros inhacaensis*, *Drypetes natalensis*, *Euclea natalensis* subsp. *natalensis*, *Heywoodia lucens*, *Hymenocardia ulmoides*, *Inhambanella henriquesii*, *Manilkara concolor*, *Millettia sutherlandii*, *Morus mesozygia*, **Olea capensis*, *Podocarpus falcatus*, *Pteleopsis myrtifolia*, **Rawsonia lucida*, *Stangeria paradoxa*, *Strychnos decussata*, *S. mitis*, *Trichilia emetica*, *Vepris undulata*, *Zanthoxylum capense* and *Ziziphus mucronata*.

11. SOUTH AFRICA, Lebombo Range, E. of Ingwavuma (SE 2732), 305 m alt., in dense semi-evergreen bushland with stunted emergent trees up to 7 m tall (WHITE, 1983a : 200; MS., 1973 : 192). Associates include : *Acacia ataxacantha*, *Aloe marlothii*, *Bauhinia galpinii*, *Canthium ventosum*, **Celtis africana*, *Chaetacme aristata*, *Combretum apiculatum*, *Diospyros dichrophylla*, *Dombeya rotundifolia*, *Euclea divinorum*, *E. racemosa* subsp. *daphnoides*, *Euphorbia ingens*, *Galpinia transvaalica*, *Heteropyxis natalensis*, *Hippobromus pauciflorus*, **Maytenus undata*, *Sclerocarya caffra*, *Sideroxylon inerme*, *Trichilia emetica*, *Turraea obtusifolia*, *Xeromphis rudis*, *Zanthoxylum capense*, *Ziziphus mucronata* and *Z. rivularis*.

12. SOUTH AFRICA, near Tugela Ferry (SE 2830), in degraded semi-evergreen bushland with scattered small emergent trees on badly eroded north-facing slope (WHITE, MS., 1973 : 233). Associates include : *Acacia nilotica*, *A. tortilis*, *Berchemia discolor*, *Diospyros lycioides* subsp. *sericea*, *Dombeya cymosa*, *Euclea racemosa* subsp. *daphnoides*, *Euphorbia tirucalli*, *E. triangularis* (locally abundant), *Maerua angolensis*, *Opuntia* sp. (naturalized) and *Pappea capensis*.

13. SOUTH AFRICA, Mtunzini (SE 2831), 20 m alt. in rather open dune forest (WHITE, MS., 1973 : 154). Associates include : *Brachylaena discolor*, *Diospyros lycioides* subsp. *sericea*, *D. villosa*, **Ekebergia capensis*, *Gardenia thunbergii*, *Hyphaene coriacea*, *Schefflera umbellifera*, *Strelitzia nicolai*, *Turraea floribunda* and *Zanthoxylum capense*.

14. SOUTH AFRICA, Umdoni Park (SE 3030), 50 m alt., in 18 m tall coastal forest on Table Mountain Sandstone (WHITE, MS., 1973 : 147). *Brachylaena discolor*, *Bridelia micrantha*, **Celtis africana*, *Chaetacme aristata*, *Chrysophyllum viridifolium*, *Dahlgrenodendron natalense*, *Diospyros natalensis*, *D. scabrida*, *D. villosa*, *Euclea natalensis* subsp. *natalensis*, **Halleria lucida*, *Harpephyllum caffrum*, *Protorhus longifolia*, **Rapanea melanophloeos*, *Scolopia mundii*, *Strelitzia nicolai*, *Syzygium cordatum*, *Trichilia dregeana*, *Turraea floribunda* and *Zanthoxylum capense*.

15. SOUTH AFRICA, in gorge of Umzinkulu River, near Gibraltar (SE 3030), in dense semi-evergreen bushland (WHITE, MS., 1973 : 252). Associates include : *Aloe arborescens*, *Bauhinia natalensis*, *Diospyros simii*, *D. villosa*, *Dombeya cymosa*, *Euclea undulata*, *Euphorbia tirucalli*, *Heteropyxis natalensis*, **Nuxia floribunda*, *Pappea capensis*, *Protorhus longifolia*, *Tarchonanthus camphoratus* and *Tecomaria capensis*.

16. SOUTH AFRICA, Umtamvuma Nature Reserve (SE 3130), in rather broken forest with an irregular canopy 16-28 m high (WHITE, MS., 1973 : 261). Associates include : *Acridocarpus natalensis*, *Bequaertiodendron natalense*, **Celtis africana*, *C. gomphophylla*, *Chaetacme aristata*, *Chrysophyllum viridifolium*, *Cnestis natalensis*, *Cola natalensis*, *Cordia caffra*, *Croton sylvaticus*, *Dalbergia arbutifolia*, *D. obovata*, *Diospyros natalensis*, **Ekebergia capensis*, *Entada spicata*, *Ficus bizanae*, *F. capensis*, **Halleria lucida*, *Harpephyllum caffrum*, *Heywoodia lucens*, *Kiggelaria africana*, *Macaranga capensis*, *Millettia caffra*, **Olea capensis*, *Oncinotis tenuiloba* (inhandensis), *Phyllanthus discoideus*, *Protorhus longifolia*, *Strychnos mitis*, *Trichilia dregeana*, *Vitellariopsis marginata*, **Xymalos monospora*.

17. SOUTH AFRICA, Keiskama River Valley (SE 3327) in semi-evergreen bushland and thicket (WHITE, MS., 1973 : 459). The main canopy is at 4-6 m, locally with a dense stocking of emergent cactoid Euphorbias up to 8-10 m tall. Associates include : *Aloe ferox* (where canopy is light), *Azima tetracantha*, *Boscia oleoides*, *Canthium obovatum*, *Chaetacme aristata*, *Calpurnia aurea*, *Dovyalis zeyheri*, *Ehretia rigida*, *Entada spicata*, *Euclea undulata*, *Euphorbia grandidens*, *E. tetragona*, *E. triangularis*, *Grewia occidentalis*,

Heteromorpha arborescens, *Homalium rufescens*, *Maytenus peduncularis*, **M. undata*, *Olea europaea*, *Pappea capensis*, *Plumbago auriculata* (capensis), *Putterlickia pyracantha*, *Rhus* spp., *Schotia afra*, *S. latifolia*, *Tecomaria capensis* and *Vepris undulata*.

In the nearby Fish River valley (SE 3326) at altitudes between 100 and 450 m where the rainfall is only 350-500 mm per annum, *Ptaeroxylon* is one of the most abundant trees and is associated with many of the species mentioned above, as well as *Brachylaena ilicifolia*, *Carissa haematocarpa*, *Crassula ovata*, *Euphorbia bothae*, *E. pentagona* (local), *Grewia robusta*, *Portulacaria afra* (dominant) and *Rhigozum obovatum* (ACOCKS, 1988 : 61).

18. SOUTH AFRICA, Fort Grey Forest (SE 3327), 100 m alt. In short dry forest, 12-15 m tall (WHITE, MS., 1973 : 438). Associates include : *Brachylaena elliptica*, *Buxus macowanii*, *Calpurnia aurea*, *Calodendrum capense*, **Cassine aethiopica*, *C. crocea*, **Celtis africana*, *Chaetacme aristata*, *Cordia caffra*, **Cussonia spicata*, *Dalbergia obovata*, *Diospyros dicrophylla*, *D. natalensis*, *D. simii*, **D. whyteana*, *Dombeya cymosa*, **Ekebergia capensis*, *Encephalartos altensteinii*, *Entada spicata*, *Euclea racemosa* subsp. *macrophylla*, *Euphorbia tetragona* (in gaps), *Ficus thonningii*, *Gardenia neuberia*, *G. thunbergia*, *Harpephyllum caffrum*, *Hippobromus pauciflorus*, *Linociera foveolata*, *Nuxia congesta*, **Olea capensis*, *O. europaea*, *O. woodiana*, *Podocarpus falcatus* (young plants only), *Protorhus longifolia*, *Rhus chirindensis*, *Schotia latifolia*, *Scolopia zeyheri*, *Scutia myrtina*, *Sideroxylon inerme*, *Strychnos henningsii*, *Teclea natalensis*, *Tecomaria capensis*, *Umtiza listerana* and *Vepris undulata*.

19. SOUTH AFRICA, Alexandria forest (SE 3326), *Ptaeroxylon* is locally abundant in this forest (K. VON GADOW pers. comm.; ACOCKS, 1988 : 20) but there is little precise information. Rainfall is 650-800 mm per annum and well distributed throughout the year. The canopy varies from 8-18 m tall and most of the trees are festooned with lichens. The most abundant trees include **Celtis africana*, *Cordia caffra*, **Olea capensis*, *Podocarpus falcatus*, *Strychnos henningsii* and *Vepris undulata*.

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Une espèce nouvelle de *Malleastrum* (*Meliaceae*) de Madagascar

J.-F. LEROY & M. CHEEK

Résumé : Description d'une nouvelle espèce de *Malleastrum*, *M. sepaliferum*, se distinguant aisément par des caractères originaux dans le genre, à savoir le calice membraneux à lobes foliacés de grande taille et des bractéoles linéaires très longues.

Summary : Description of a new species of *Malleastrum*, *M. sepaliferum*, easily distinguished by characters unusual for the genus : a membranaceous calyx with large leaf-like lobes, and very long linear bracteoles.

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Le genre *Malleastrum* fut établi par l'un de nous (J.-F. LEROY) en 1964, par ségrégation du genre *Cipadessa* sect. *Malleastrum* Baillon (1874). Les statuts d'une première série de 11 espèces de Madagascar, dont une présente aussi aux Comores, furent alors publiés. Par la suite F. R. FOSBERG décrivit une espèce nouvelle d'Aldabra. Compte tenu du matériel en collection un grand nombre d'espèces nouvelles restait à publier, ce que J.-F. LEROY annonçait à l'époque et une autre série est maintenant en cours de publication. Une première note de cette série faisant connaître 3 espèces a paru récemment (LEROY, 1989). L'espèce remarquable, qui fait l'objet du présent article, avait retenu l'attention de J.-F. LEROY par certains caractères très affirmés (calice membraneux à lobes foliacés de grande taille, bractées linéaires très longues, ovaire à 4(-5) loges) et un nom lui avait été donné *in herbario* (*M. sepaliferum*) dès 1964.

Indépendamment, M. CHEEK ayant eu l'occasion, en 1988, de pouvoir étudier des échantillons de cette espèce provenant de Nosy Mangabe, l'a aussi reconnue comme nouvelle ; une étude avait même été rédigée, par ses soins, en vue de publication. D'un commun accord, nous avons décidé, en conséquence, de nous associer pour publier cette nouvelle espèce sous l'appellation qui lui avait été donnée en 1964.

Le matériel étudié récemment par M. CHEEK a été collecté, en février 1988, par G. SCHATZ, du Missouri Botanical Garden, en compagnie de J. et S. DRANSFIELD, D. SIMPSON et M. STANFORTH des Royal Botanic Gardens, Kew. Malheureusement, bien qu'un grand nombre de parts aient été faites, beaucoup ont été attaquées par des moisissures (*fide* G. SCHATZ) et seulement une petite quantité de matériel a pu être sauvée, une partie sous la numérotation de M. CHEEK. L'espèce a été retrouvée depuis, dans la même localité, en fleurs (mai 1988) et en fruits (janvier 1989), ces derniers étant remarquables par leur pilosité.

Malleastrum sepaliferum J.-F. Leroy & Cheek, *sp. nov.* — Fig. 1.

Foliola 3-5(-7) nervatione bene notata. Flores comparate multi in fasciculos cymosos breves dispositi. Ovarium 4-(5)-loculare. Fructus tomentosus; semina testa dura. Species notabilis bracteis longissimis, calycis lobis foliaceis membranaceis valde evolutis, pilis sparsis instructis.

Arbuste de 1-3 m ou arbre de 8-10 m de hauteur. Rameaux à écorce grisâtre, à crêtes longitudinales peu élevées, éparpillées, finement pubescents à petits poils courts, adultes glabres à lenticelles claires, ovales, peu visibles; jeunes à lenticelles non manifestes \pm circulaires, couverts de poils atteignant 0,5 mm. Feuilles à 3-5-7 folioles, la dernière plus développée, de 8-15 \times 6-12 cm. Folioles à limbe chartacé, largement à étroitement elliptique à légèrement ové, arrondi-obtus à atténué subacuminé particulièrement sur les plus longues folioles au sommet, aigu à décurrent à la base, de 2,5-7(-10) \times 1,3-3(-4) cm, légèrement révoluté, parfois ondulé sur les bords, glabre sauf sur la nervure médiane et à petits poils courts dressés en dessous sur les nervures secondaires, vert \pm foncé brillant en dessus, plus pâle et mat en dessous, à ponctuations pellucides rares. Nervure primaire plate en dessus à légèrement proéminente. Nervures secondaires nombreuses, 12-14 paires, et réticulum finement marqué des deux côtés. Pétiole canaliculé en dessus, convexe en dessous, de 0,6-3 cm, courtement pubescent; pétiolule pubescent, plat en dessus, convexe en dessous, de ca. 0,75 \times 1-12 mm, plus long dans les folioles terminales.

Inflorescences cymeuses, pauciflores, groupées par 1-5 à l'aisselle des feuilles terminales et des bractées au sommet des rameaux; pédoncules généralement aplatis dorsiventralement, de 14-26 \times 1,5 \times 0,5 mm, pubescents, parfois à lenticelles claires, elliptiques, lisses, ca. 0,2 \times 0,1 mm. Bractées et bractéoles linéaires, de 1,75-5 \times 0,3-0,5 mm, velues à poils raides, épars. Boutons largement elliptiques, enveloppés par le calice. Fleurs de 4-5 mm, à pédicelles verts, \pm épais, de 1-3 \times 1,5-2 mm, articulés, velus. Calice vert, membraneux, en coupe haute de 1,5 mm, large de 2,5-3 mm, parsemé de poils raides apprimés ou dressés, glabre intérieurement; 5-(6) lobes foliacés, remarquablement développés, longuement triangulaires aigus, hauts de 2-5 mm, larges de 0,75-1,5 mm à la base. Corolle à 5 pétales blancs, valvaires redoublés, réfléchis vers l'arrière à l'anthèse, largement elliptiques, cucullés au sommet, de 4-4,7 \times 1,5-1,8 mm, glabrescents vers le sommet sur la côte médiane et la marge, glabres intérieurement, papilleux sur les bords. Etamines 10, à filets longs de 2,5 mm, soudés sur 1/2 ou 2/3 de leur longueur en un tube staminal cylindrique, campanulé, large de 2,5 mm, glabre extérieurement, velu hirsute intérieurement sur la partie libre des filets terminée par des appendices \pm égaux, filiformes, parfois tortillés au sommet de 1-1,8 mm, souvent plus longs que les anthères, glabres, papilleux; anthères jaunes, elliptiques, de 1,1 \times 0,4 mm, mucronulées au sommet, glabres, parfois à poils épars. Pistil atteignant \pm les anthères, haut de 2,6 mm, large de 1,8 mm à la base, pourvu de très longs poils jaunes soyeux longs de 0,6-0,8 mm; ovaire conique-trigone, de 1,2 \times 1,2 mm, à 4-(5) loges biovulées, les ovules superposés; style droit, glabre sauf à la base, haut de 1 mm, de 0,2 mm de diamètre; tête du style subglobuleuse, de 0,3 \times 0,5 mm; stigmate petit, obscurément 4-lobé, de 0,1 mm de diamètre, déprimé au centre.

Fruit subglobuleux, généralement terminé en pointe déjetée au sommet, de 1-1,5 cm de diamètre, densément tomenteux à poils longs épars et poils courts plus denses; calice persistant. Péricarpe épais de 0,7 mm. Graines, 1-3, une par loge, subangulaires, marron foncé,